Marine Research

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Marine Research
1958 No. 7

Plant Production in the Northern North Sea

By J. H. STEELE, B.Sc.

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Plant Production in the Northern North Sea

INTRODUCTION

n an earlier paper (Steele, 1956) estimates were made of the production of organic matter at one ion, the Fladen Ground, in the centre of the northern North Sea. They were based on the changing cal distribution of phosphate and on the part played in these changes by the vertical mixing of the r. Since these results provided a fairly coherent description of the production cycle in terms of the cal environment, it was decided to try and apply this method to the whole of the northern North To this end, sampling for temperature, salinity, phosphate, oxygen, chlorophyll and dry weight, ed part of surveys of the area carried out during 1954-56.

he Fladen Ground was chosen originally for this type of work as it was an area where lateral water ges were expected to be small during most of the year and so vertical mixing would be the only rtant hydrographic factor. For the rest of the area, lateral changes may be significant and a etical study has been made of the hydrography (Steele, 1957a).

is still difficult, however, to interpret particular estimates of phosphate consumption and to decide e validity of each measure of production. For this reason a theoretical study has been made of the s of nutrients, plants and animals so that expected values of production could be found for given tions of vertical mixing. This approach provides its own special problems and so, in the end, there straightforward comparison of predicted and observed production rates. The aim, rather, is to see at extent there is consistency between the various modes of approach and to use the inconsistencies ggest further investigations.

he development of the theoretical model is given first, together with its detailed relevance to certain cular positions in the northern North Sea; then a general chart of the expected values of yearly ction is given for the whole area. In the second part, the results of sampling are discussed and the ved values of production are compared with the theory.

Part I

A THEORY OF THE PRODUCTION CYCLE

he production of organic matter in the sea is controlled by many complex factors. Some of these ell known, sunlight, grazing by herbivores, water mixing, turbidity and nutrients; others, such as olic relations between plant species, are still a matter for conjecture. Yet even with the accepted es, the exact nature of the relationships and their quantitative expression are not satisfactorily ished.

o set up a mathematical model of the process of production, it is necessary to put some of these y defined relations into a rigid structure and to neglect the others completely. Such a procedure rs arbitrary but it is only in this way that the logical consequences of these relations can be explored. is the purpose of this section to study some of these factors and in particular the effects of variations tical mixing of the water column. Previous studies of this type have been made by Riley (1946, 1947), , Stommel and Bumpus (1949) Cushing (1955) and Steele (1956); the general problems are reviewed ley (1953) and Steele (1959). These analyses of particular observed seasonal cycles have been made ting up equations which will reproduce the observed changes and such work has shown that it is le to explain the main features of population changes in terms of the few factors already mentioned. ne drawback of this approach is that these factors are all varying throughout the year and it is lt to disentangle their individual effects. To obtain insight into the part played by each factor, it essary to construct a completely theoretical model in which each factor can be varied in turn.

Such a model must be a simplified picture of the complex sequence of events in the sea, and s population changes which it predicts cannot be accepted *a priori*. It is only if the general featu the results appear credible that the details can also be considered to have some validity.

Since it is intended to apply the results of this work to investigations in the northern North Sea postulates are constructed from this point of view.

(1) 1 POSTULATES

(1) 1.1 Vertical Mixing

During winter, in most of the northern North Sea, the water column is homogeneous from su to bottom. Then during April a thermocline is formed which lasts till the autumn, when it is br down. The model will be concerned with the period when there is a thermocline and the situation be idealised by considering the water column to be in two homogeneous layers divided at 40 m (Fig

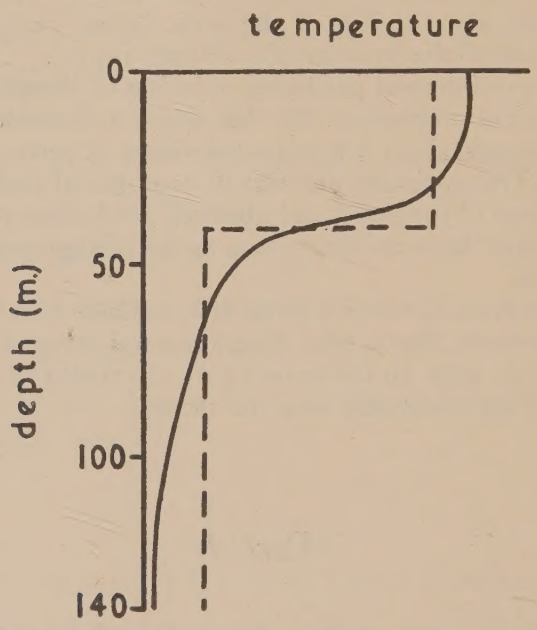

Fig. 1 An observed and idealised thermocline.

There will be a rate of mixing m between the two layers which usually will be kept constant throug a season to produce a cycle of production. By varying m different cycles will be obtained.

The three artificial features of this postulate are

i. the thermocline has a fixed depth;
ii. the water layers above and below it are homogeneous;
iii. the rate of mixing is constant.

These imply that the other features, phosphate and plant population, will have a similar distrib and the most important artificiality here is that the plants will have the same density from 0 to whereas it is usually found that there are quite large variations of concentration with depth (Riley 1949; Steele, 1956, 1957b).

(1) 1.2 Light, Transparency and Photosynthesis

The compensation depth is defined as that level in the sea at which the light is just sufficie support a rate of photosynthesis which balances the loss due to respiration. This depth depends o light intensity at the surface and the transparency of the water.

the northern North Sea the mean daily depth probably varies from 20 to 50 m. The euphotic zone it defines is shallow during the spring outburst when the plants themselves reduce the transparency, increases in depth during the summer when the plant density is lower and the light stronger.
this work, these seasonal variations in light and transparency will be ignored. It will be assumed he 0-40 m layer corresponds to the euphotic zone and that the photosynthetic rate in this layer is ant except for the effects of nutrient depletion. The constant rate, K, is chosen at 0·30 g carbon/g carbon/day, which is the mean production rate during the spring outburst in 1956 calculated from xperiments and chlorophyll data (Steele, 1957b), using a conversion factor

$$1 \text{ mg chlorophyll} = 54 \text{ mg carbon.}$$

factor, given by Riley *et al* (1949), was adopted for the Fladen work and will be used throughout aper.

3 Nutrient Deficiency

here is a considerable range of opinion concerning the way in which a low nutrient concentration e water limits the rate of photosynthesis (Steele, 1959). From experiments by Ketchum (1939), (1946) chose as the simplest expression of phosphate effect, a photosynthetic rate given by

$$P_k = \frac{p}{0{\cdot}55} K$$

the phosphate concentration $p < 0{\cdot}55$ μg.at./l.
here are two arguments against this linear relationship (A, Fig. 2). The first arises from evidence he phosphate concentration per plant cell decreases as the concentration of nutrient in the water

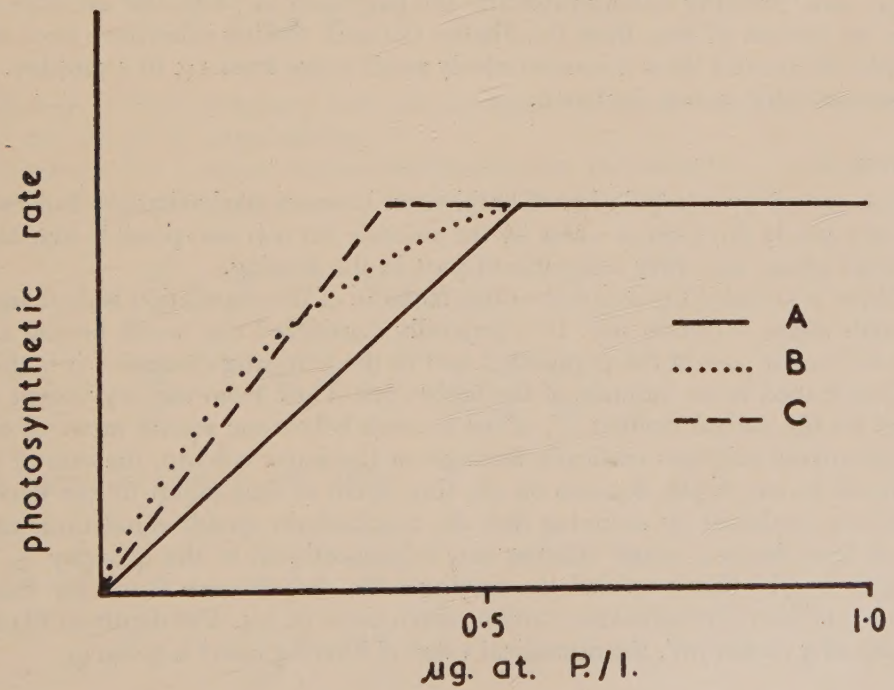

Fig. 2 Possible effects of nutrient deficiency on photosynthetic rate.

ises. This would imply that the limiting effect of nutrients occurred more gradually in a curvilinear such as B). Secondly, Ketchum's experiments were made with a diatom but the nutrient limitation mainly the summer forms of plants which are largely flagellates. The results of Barker (1935) t that the limiting concentration for flagellates may be about 0·25 μg.at./l.

Once more, there is here a collection of somewhat vague evidence on phosphate limitation a rather arbitrary decision must be made to give a quantitative representation. In this work, as a promise, a linear effect (C), will be used with a lower threshold, 0·40, than in Riley's formula; the is given in

$$p_h = K \ , \ p \geqslant 0{\cdot}40 \ \mu g.at./l$$

$$p_h = \frac{p.K}{0.40} \ , \ p < 0{\cdot}40 \ \mu g.at./l$$

(1) 1.4 Temperature Effects on Respiration

A principal feature of the metabolism of the plants is their respiration. This will depend on temp ture, and Riley has given the following formula,

$$r_T = 0{\cdot}0175 \exp(0{\cdot}069T)$$

where r_T is the respiratory coefficient in g carbon per day per g of plant carbon at temperature T.

By assuming a mean temperature of 10°C in the euphotic zone $r_T = r = 0{\cdot}035$ and this con value will be used throughout the model.

(1) 1.5 Sinking Rate

The rate at which plants sink through the water may vary with their physiological condition also with the changes in density and viscosity of the water due to varying temperature. Further, diff plant species may have differing sinking rates and the flagellates in particular are able to propel th selves. However, by the use of data from the Fladen Ground, sinking rates have been deduced (St 1956, 1957b) which in general show a comparatively small range from 1·4 to 4·9m/day. Once more the model, a constant value, $v = 3$, is chosen.

(1) 1.6 Grazing

The plants are grazed by a population of herbivores. It seems likely that the bulk of this grazi done by means of a steady filtration of water by the animals but it is also possible that searching for eating of individual plants may play a significant part in the grazing.

The zooplankton is sampled by nets and so this measure of the population is dependent on the n selection of animals above a certain size. It is generally considered that a silk having about 60 me per inch retains the major part of the population and in the following discussion it is this portion o zooplankton which is used as an estimate of the herbivores. Thus, from the dry weight of a net ha value is obtained for the carbon content, Z, of the animals below one square metre of surface.

Since the zooplankton migrates vertically throughout the water column, the rate at which the p population is grazed at any depth depends on the time spent at that depth by the herbivores.

These factors are combined by assuming that the zooplankton spends equal times at all depths consists purely of filter feeders, whose filtering rate is proportional to the quantity Z. From the data (Steele, 1956, 1957b) that provided the sinking rates, values were found for filtering rates ranged from 1·0-7·7 m^3/day/g zooplankton carbon with a mean of 3·4. The depth on Fladen is 140 m to retain Z in units of g carbon/m^2, the numerical value of filtering rate f is given as

$$\frac{3{\cdot}4}{140} = 0{\cdot}024$$

(1) 1.7 Consumption of Phosphorus

Since phosphate occurs as a factor in the formula for photosynthesis it is necessary to set up equation for this quantity. The simplest assumption is that the rate at which phosphate is remove

lants is proportional to the rate of carbon uptake, the proportion being that in which phosphorus arbon have been found in chemical analyses of phytoplankton. In the units used this is

$$1 \text{ g carbon/m}^3 \equiv 0.774 \ \mu\text{g.at.phosphorus/l.} = c$$

3 Regeneration of Phosphorus

he main difficulty in discussing phosphate changes is the role of regneration in the euphotic zone. s been suggested that this rate is very large (Cushing, 1955) but the evidence of C^{14} experiments e Fladen Ground does not support this conclusion (Steele, 1957b). For this reason, regeneration in uphotic zone is neglected except for the regeneration due to plant respiration.

(1) 2 EQUATIONS

1 The Equations for Phosphate-Phosphorus and Plant Carbon

ith these postulates the equations for phosphorus and plants can now be set up. Following Riley 1949) the equations for the rate of change of plants, P' in g carbon/m³ and phosphate-phosphorus, μg.at./l, at any depth z, are

$$\frac{\partial P'}{\partial t} = (p_h - r - f\mathcal{Z})\,P' - v\frac{\partial P'}{\partial z} - \frac{\partial}{\partial z}\left(\frac{A_z}{\rho}\,\frac{\partial P'}{\partial z}\right) \quad .. \quad .. \quad .. \quad (1)$$

$$\frac{\partial p'}{\partial t} = -C(p_h - r)\,P' - \frac{\partial}{\partial z}\left(\frac{A_z}{\rho}\,\frac{\partial p'}{\partial z}\right) \quad .. \quad .. \quad .. \quad .. \quad (2)$$

is the coefficient of eddy diffusivity and ρ is the density of the water. The terms containing these s represent the effects of water mixing.

cause of postulate (1) 1.1 about the vertical distribution, the values of P' and p' required are the concentrations P and p from 0 to 40*m*. Thus equations (1) and (2) become

$$\frac{dP}{dt} = (p_h - r - f\mathcal{Z})P - \frac{vP}{40} - \frac{1}{40}\left(\frac{A_z}{\rho}\,\frac{\partial P'}{\partial z}\right)_{z=40} \quad .. \quad .. \quad .. \quad (3)$$

$$\frac{dp}{dt} = -c\,(p_h - r)\,P - \frac{1}{40}\left(\frac{A_z}{\rho}\,\frac{\partial p'}{\partial z}\right)_{z=40} \quad .. \quad .. \quad .. \quad .. \quad (4)$$

ıe mixing terms are put in the form

$$\frac{1}{40}\left(\frac{A_z}{\rho}\,\frac{\partial P'}{\partial z}\right)_{z=40} = m\,(P - P_o)$$

$$\frac{1}{40}\left(\frac{A_z}{\rho}\,\frac{\partial p'}{\partial z}\right)_{z=40} = m\,(p - p_o)$$

are the changes across 40 m with P_o and p_o as the concentrations in the lower layer; m is now the ed coefficient of vertical mixing.

ıce the lower layer is homogeneous it is assumed that plants which pass down into this layer are l evenly throughout it and their concentration is negligible; that is $P_o = o$.

rther, it is assumed that the phosphate concentration in the lower water remains constant at its value of $p_o = 0.70$ μg.at./l. In fact, for these waters where there is little mixing, the lower water

concentration rises to about 0·90 μg.at./l in summer; when the mixing is high it falls to about 0·50 μg.a

In a similar way, the term for sinking has become

$$\frac{v \cdot P}{40}$$

which expresses the decrease in the mean concentration in the upper 40 m.

It is now possible to write down the equations for P and p in the upper 40 m using the values give the postulates,

$$\frac{dP}{dt} = (0{\cdot}19 - 0{\cdot}024Z - m)P \qquad , p \geqslant 0{\cdot}40$$

$$= (0{\cdot}75p - 0{\cdot}11 - 0{\cdot}024Z - m)P \qquad , p < 0{\cdot}40$$

$$\frac{dp}{dt} = -0{\cdot}205\,P + m(0{\cdot}70 - p) \qquad , p \geqslant 0{\cdot}40$$

$$= -(0{\cdot}58\,p - 0{\cdot}027)P + m\,(0{\cdot}70 - p) \qquad , p < 0{\cdot}40$$

(1) 2.2 The Equation for Zooplankton

An equation for the changes in the herbivores Z will be of the form

$$\frac{dZ}{dt} = growth - loss$$

The growth is given by the rate at which animals reach the size where they are retained by th together with their increase in weight thereafter. The loss is due to predation by those carnivores, su Sagitta and herring, which feed on herbivores. Not merely are such components very complex but to the predation factor, this equation would, in turn, depend on another equation for predators, so on.

The simplest way of avoiding this complexity is to set up an empirical equation which will satisf same observed conditions and whose variations should follow the generally expected pattern. Fo purpose, the most adequate data are the average values from a group of four stations on Fladen in In Fig. 3, smooth curves have been drawn through the values of phytoplankton and zooplankton.

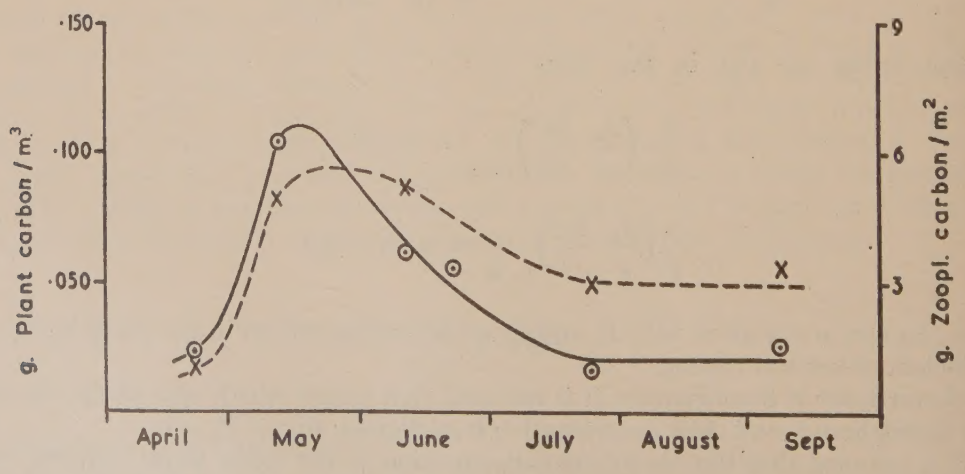

Fig. 3 Plants (O) and animals (X) on Fladen in 1953.

ıe first feature of these curves is that $dZ/dt = o$ on two occasions and on these occasions the values P are $o{\cdot}35$ and $o{\cdot}45 \times 10^3$ respectively. This suggests the following equation,

$$\frac{dZ}{dt} = A(400P - Z^2)$$

the slope of the 'Z-graph' on 11th May, a value of A is obtained which gives

$$\frac{dZ}{dt} = 4P - o{\cdot}o1Z^2 \qquad .. \quad .. \quad .. \quad .. \quad .. \quad (9)$$

ıough this equation is empirical it is possible to provide an interpretation of the two terms on the ıand side. The first, which is the growth term, implies that the rate of increase depends solely on :e of the plant population and not on the herbivore stock itself. This result may reflect the fact that ying in *Calanus* depends on the food available (Marshall and Orr, 1955), and that recruitment is ndependent of the parent stock. There is evidence for a similar state of affairs in the recruitment ıng fish (Parrish, 1956).

ıe second term would imply that the rate at which the stock, Z, was being grazed was proportional in other words that the quantity of predators was proportional to the quantity of herbivores. This e may reflect the fact that numbers of predators tend to increase and decrease with the numbers ir prey although with a time lag.

his way it is possible to provide some basis for the form of the equation. With such a background ıs probable that, for different curves of plant populations, the changes in the predicted herbivore ıtrations will be in the right directions.

(1) 3 THEORETICAL CYCLES OF PRODUCTION WITH VARIABLE MIXING

Steady State Conditions

e first use that can be made of these equations is to solve them for the case where the left-hand re zero. This means that the concentrations of phosphate, plants and animals are assumed to be nt, and for any value of the mixing coefficient m, these constant values can be derived. In Fig. 4, re graphed against m, together with the values of the corresponding rate of production.

e concept of a steady state is an ideal which will never be found in nature, but the nearest ximation to it will occur in summer after the spring outburst and before the autumn breakdown. ; time mixing has two functions. Without it, no nutrients would be transported upwards to carry duction, but as mixing increases, more and more plants are removed by this mechanism from the tic zone. The expected result of these processes is shown by the model; there is a rate of mixing ch the rate of production is a maximum, and the plants and animals also have a maximum near ılue.

e phosphate curve shows one interesting feature; when the mixing is increased by a factor of ten ·005 to 0·05, production increases by a factor of seven, but the phosphate concentration increases over a half. The conclusion to be drawn from this is that the phosphate concentration in the tic zone during the summer is not a satisfactory index of the rate of production.

Changing Conditions

e equations (5-9) can be solved for any mixing rate m to give the cycle of events following initial of p, P and Z. Since production starts after the formation of the thermocline in early spring, the chosen correspond to winter conditions. They are, $p = 0{\cdot}70$ μg.at./l. $P = 0{\cdot}005$ g carbon/m^3, ·40 g carbon/m^3.

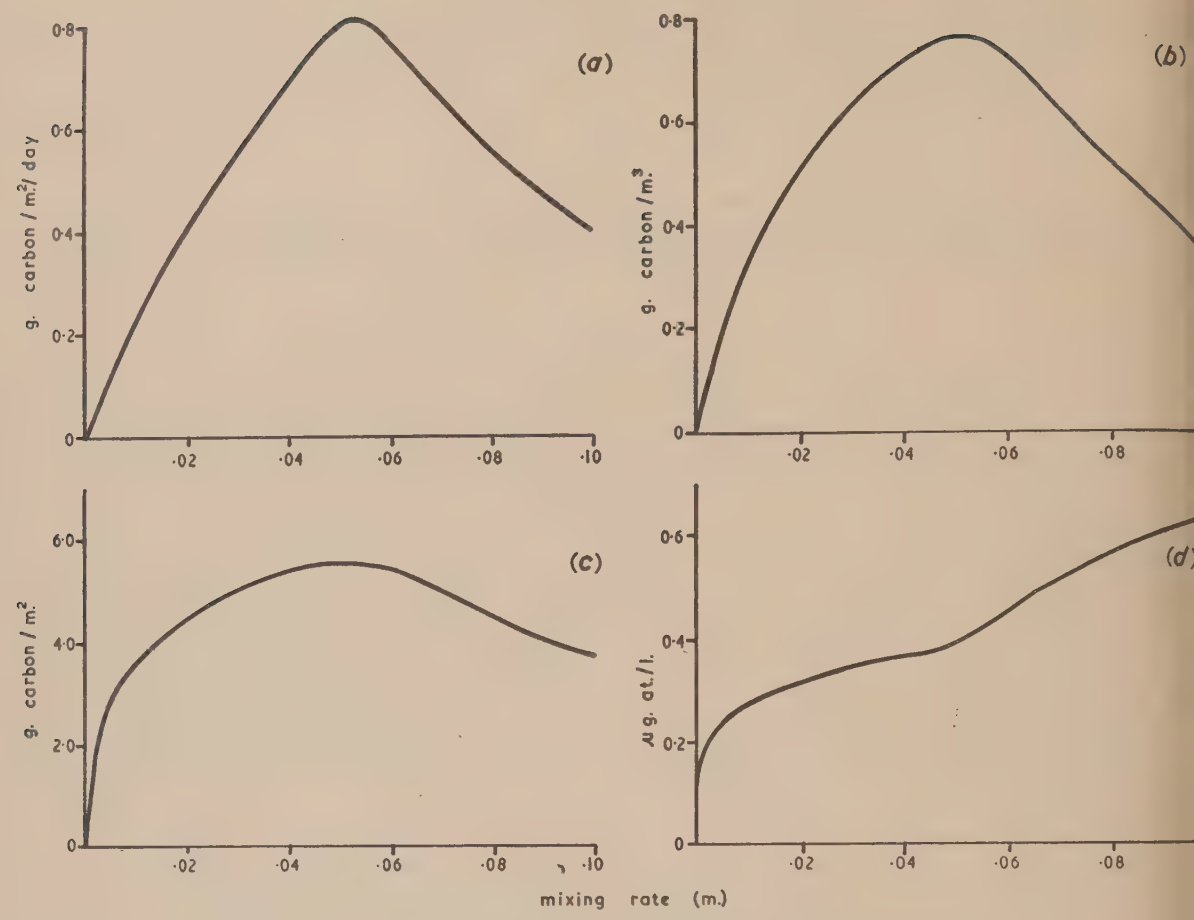

Fig. 4 Changes in steady-state conditions with mixing rate:
(*a*) production; (*b*) plants; (*c*) herbivores, (*d*) phosphate-phosphorus.

The equations cannot be solved mathematically and so a numerical step-by-step method is Four different mixing rates were chosen, $m = 0{\cdot}005$, $0{\cdot}015$, $0{\cdot}030$ and $0{\cdot}050$, which range from lo maximum steady state production, Fig. 4. The solutions for plants, herbivores and phosphorus are g in Fig. 5.

In all cases the quantities tend to the steady state values shown on the right-hand side of the gr They do not, however, approach these values smoothly, but in a series of damped oscillations. It i impossible that this could be a feature of the events in the sea; but, most likely, it is a purely mathema artifact similar to that found in the theory of servo-mechanisms. Thus it is a sign of the inadequa this mathematical model.

In Fig. 6 the rates of production are shown. The main feature to be noted is that during the s a high mixing rate gives a slower and smaller outburst because a larger proportion of the plant being mixed downwards. For the lowest and highest rates of mixing the quantities produced are at the 44th day, Fig. 7. It is only from this time onwards that the high mixing rate gives an incr production due to the increased supply of phosphate which now becomes important.

By comparison with the phosphate graphs it can be seen that the limiting action of phosph supposed here to begin at $0{\cdot}40$ µg.at./l, does not have its effect until the peak of the spring outbu past. For this, and lower, limiting values of phosphorus, it is possible to say that nutrient defic does not control the size of the spring outburst which is mainly decided by grazing and the deg mixing. After this peak has been passed, however, nutrients become of major importance and produ depends on the amounts of them transported upwards by mixing.

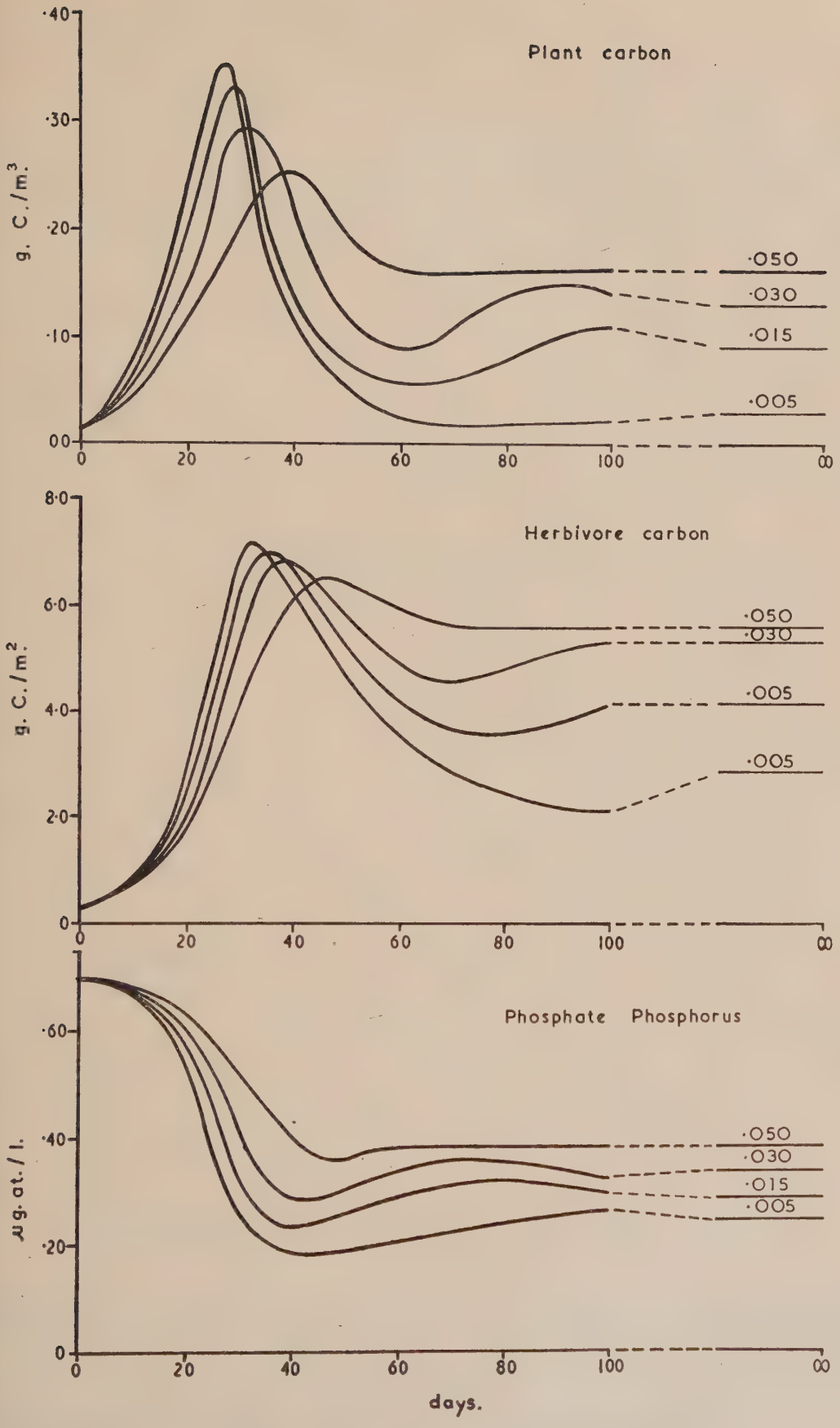

Fig. 5 Cycles for four mixing rates of: (*a*) plants; (*b*) herbivores; (*c*) phosphate-phosphorus.

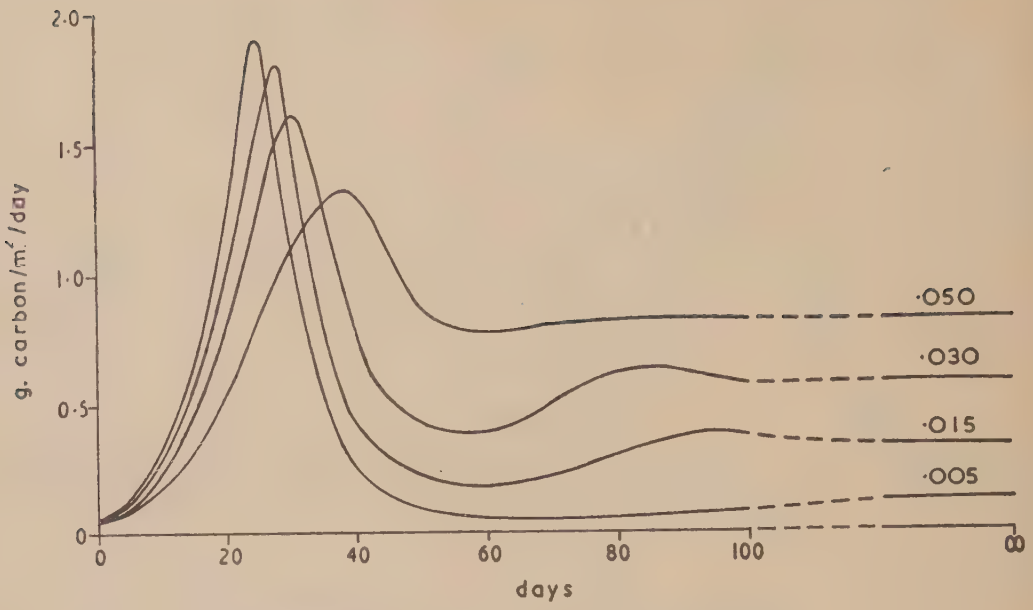

Fig. 6 The production cycles for four mixing rates.

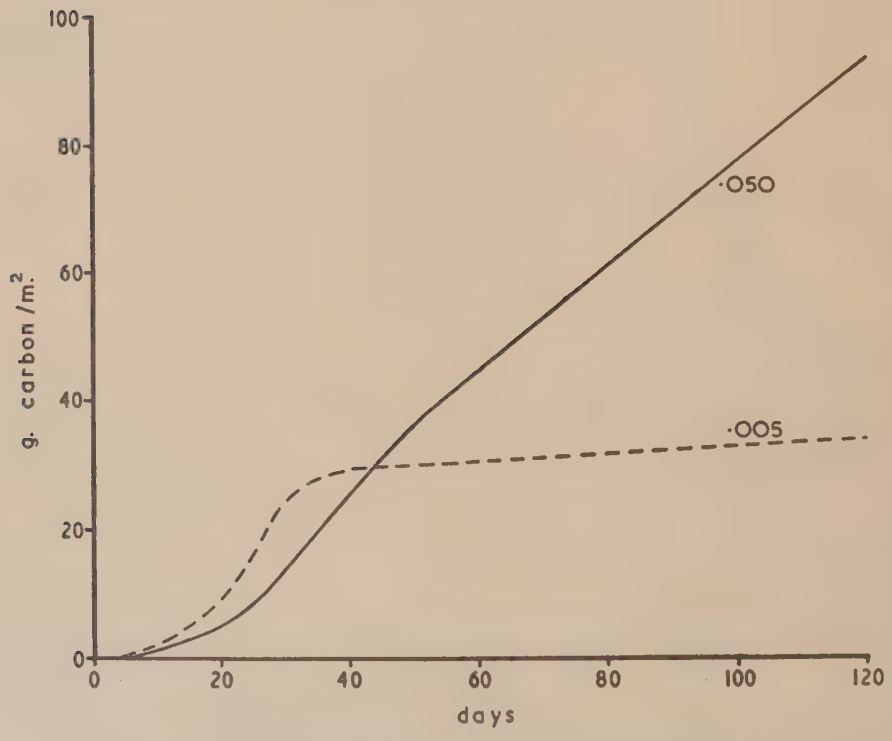

Fig. 7 Integrated production for low and optimum mixing rates.

Again it can be seen that the phosphate concentration is not a good index of production for, i spring, a high phosphate corresponds to a low rate of production, whereas in the summer the opp is true.

For this model, the values of photosynthetic, sinking, and grazing rates have been taken from for the Fladen Ground and variations in the mixing parameter *m* have been studied. Before thes compared with observations, the effects of changes in the other parameters will be discussed.

(1)4 VARIATIONS IN OTHER PARAMETERS

study these variations it was decided to calculate the cycles with new values for sinking, grazing otosynthetic rate. The mixing was taken as 0·015 and, keeping the other two at their old values, ate was first doubled and then halved. This worked satisfactorily for grazing and sinking and in a and 8b the graphs for population are compared with the original calculation. Both high sinking

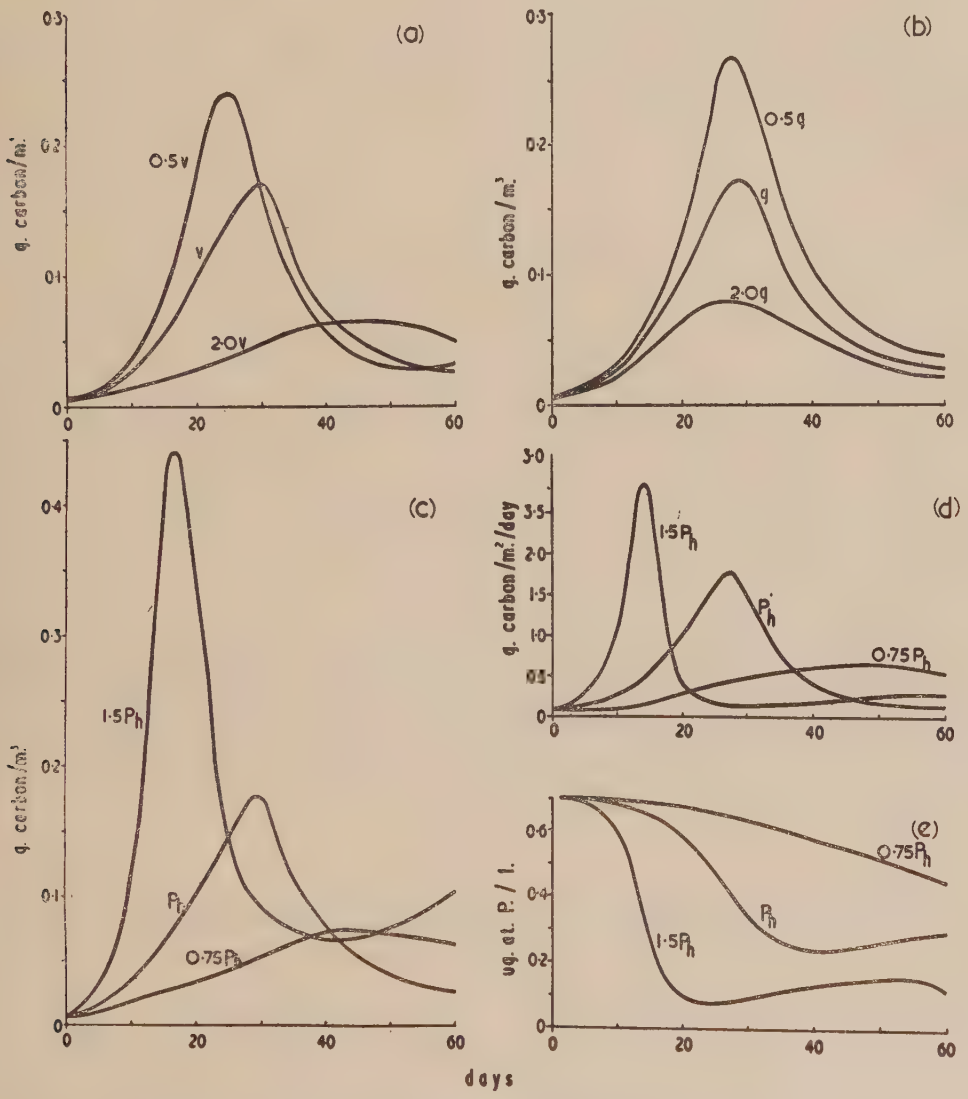

Fig. 8 Variation of the other parameters: (*a*) population cycles with changing sinking rate; (*b*) population cycles with changing grazing rate; (*c*) population cycles with changing photosynthetic rate; (*d*) production cycles with changing photosynthetic rate; (*e*) phosphate cycles with changing photosynthetic rate.

d high grazing rates give unnaturally low curves. The low rates, however, give maximum values re not improbable during the spring outburst. At this time the plants will be at their healthiest s their sinking rate might be lower. This, however, would lead to generally higher maximum ions. A more likely reason for occasional high values is lateral patchiness of zooplankton which ive small areas with an effectively lower grazing rate.

eneral, these curves show that the limits on the two parameters are not very strict, especially

for the lower ranges. Turning to the third parameter, photosynthetic rate, the opposite conclusion reached. When calculations were attempted with double and half this parameter, hopelessly unrea curves were obtained and the calculations were repeated with rates 1·5 and 0·75 of the original. these, Fig. 8c, show changes which have nearly twice the range given by Figs. 8a and 8b.

Thus it is obvious that the population curve is very sensitive to changes in photosynthetic rate. it is this parameter which is most likely to vary from day to day, due especially to changes in intensity dependent on the weather conditions. Steeman Nielsen and Jensen (1957) have pointed that, owing to surface inhibition of photosynthesis, large changes in light intensity do not pro corresponding changes in photosynthetic rate under unit surface; thus a decrease in light to one- changes photosynthesis by a factor of two-thirds only. However, from the model, it is obvious that change lasting for several days during the spring outburst would modify the population c profoundly.

There is still the question of the effect of such changing rates on the production itself and to illus these the graphs for production and nutrients are shown in Figs. 8d and 8e for the case of va photosynthetic rates. It is apparent that the changes in production are much less than those in popul although the pattern is the same. The reason for this is given by the phosphate curves which show with a high photosynthetic rate, the rapid increase in population quickly brings the phosphate below its limiting value, whereas with a low rate this value is not reached during the first two mo The result of this is that for a period of 60 days the total production due to the three rates shows comp tively small variation, being 25, 34 and 37 g C/m² for low, medium and high rates respectively. variations in photosynthetic rate can greatly change the details of the population cycle without r altering the possible production which is of course controlled by the upward mixing of nutrients.

Further variations could be worked out along similar lines; in particular combinations of, say, grazing and low sinking might give curves similar to the original so that these new values could be sidered as satisfying observed conditions within the wide limits given by the data. The model by could not decide between these values since such a choice depends on a study of changes in the det vertical distribution of the plant population, an aspect which is ruled out by postulate (1) 1.1. T one of the artificialities of the model and illustrates the limits of its use. There are other limitat principally those due to the empirical nature of the zooplankton equation which does not allow fo time lag between reproduction and effective grazing ability. Such problems may be incorporate future attempts to describe theoretically the relations between nutrients, plants and animals. The use now, will be to compare the model based on observed values of the parameters with data coll in the North Sea, letting mixing be the only variable factor.

(1) 5 EVALUATION OF THE MIXING RATE AND COMPARISON WITH FLADEN DATA

The terms which give the mixing in the original equation have the form

$$\frac{1}{40}\left(\frac{Az}{\rho}\frac{\partial Q'}{\partial z}\right)_{z=40} = m\,(Q - Q_o)$$

where Q is a mean concentration from 0 to 40m
Q_o „ „ „ „ „ 40m to bottom.

Now, for temperature T', (Steele, 1956),

$$\int_{bottom}^{40} \frac{\partial T'}{dt}\,dz = \left(\frac{Az}{\rho}\frac{\partial T'}{\partial z}\right)_{z=40}$$

comparison

$$= m \cdot 40\,(T - T_o)$$

$$m = \frac{I}{40\,\Delta t\,(T - T_o)} \int_{bottom}^{40} (T_2 - T_1)\,dz \quad \text{, approximately,}$$

T_1 and T_2 are the observed temperature distributions at the beginning and end of a time interval days.

m this formula it is possible to calculate an approximate mean value for m between any two ng dates.

e first data to be considered are from the Fladen Ground. In Table I, values of m are given for the 951-53 and 1956. It can be seen that the values are generally less than 0·006 with occasional high Thus in general the cycle on Fladen corresponds to the case of low mixing — m = 0·005.

TABLE I

Values of $m \times 10^3$ for Fladen and Inshore areas

	April	May	June	July	Aug.	Sept.	Oct.	Nov.
1951	2·5		0·8		0·2	29·8	9·5	
1952	4·4	13·5	5·8	6·0	9·4		49·0	
1953	12·8	6·0	0	0·7	4·1	2·0	16·0	
1956	5·7	41·0	5·9	1·4	6·2	0·5		
e, 1953	30	43	21	12	17	58		

s unfortunate that in 1956 there was a period of unusually high mixing during the spring outburst means that conditions were not typical during a period when sampling was fairly frequent and d C^{14} experiments (Steele, 1957b). For this reason a special calculation was made with a sequence ng rates of 0·005 — 0·040 — 0·005 to correspond to the observed changes. In Fig. 9a the resulting

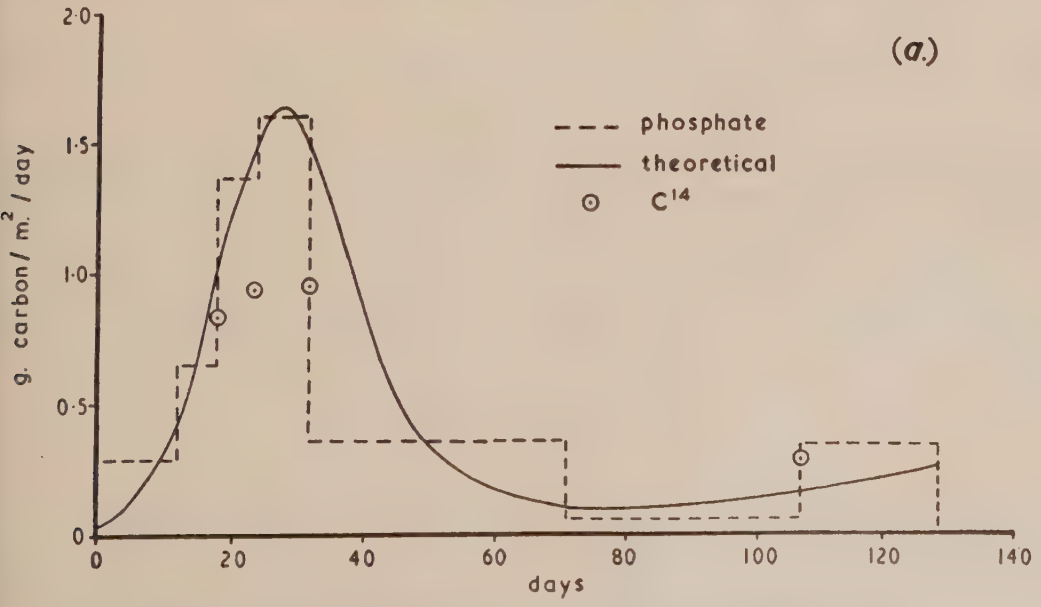

Fig. 9 (*a*) The production cycle on the Fladen Ground in 1956.

theoretical curve for production is superimposed on the production histogram obtained from phos data; also shown are values for production rate given by the C^{14} experiments.

One problem in making this comparison is that it is difficult to say when the observed produ began and thus to choose a date from which both the model and the histogram shall start. A b comparison can be seen by integrating both estimates and Fig. 9b shows that during the first 32 a very good fit would be obtained by shifting the curve by a few days. For the slower increase aft

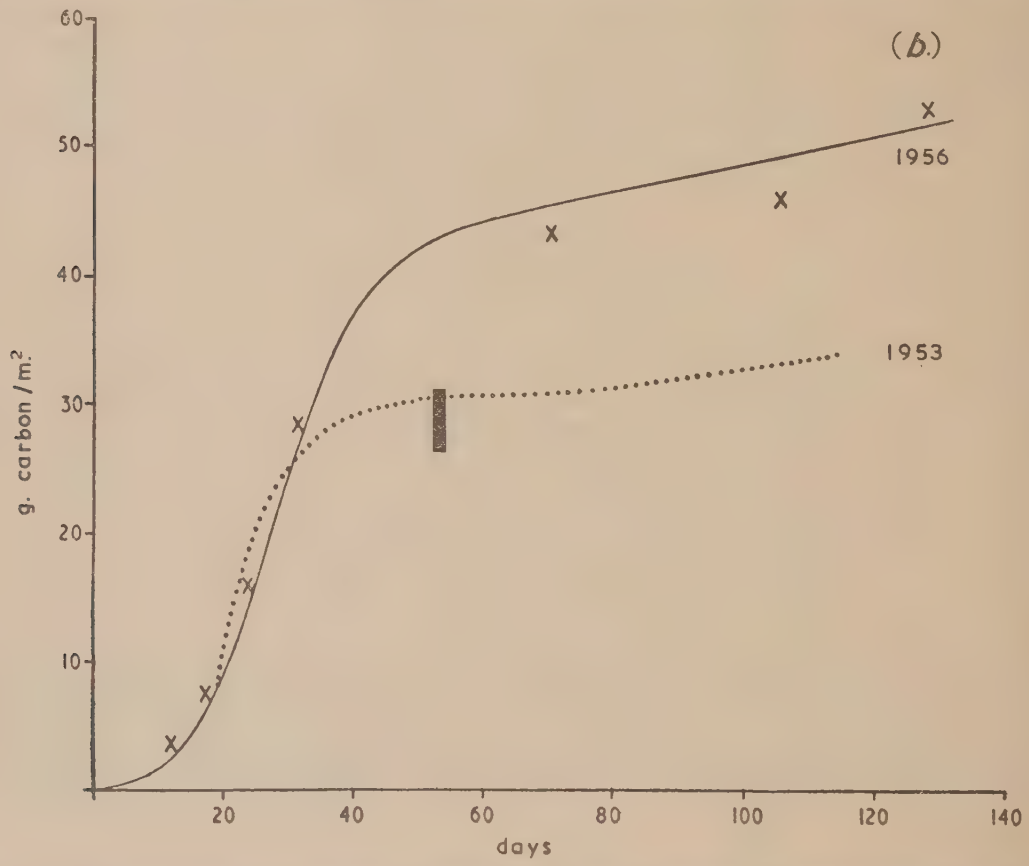

Fig. 9 (*b*) A comparison of integrated theoretical (—) and observed (X) production in 1956 and also 1953 (see text).

spring outburst, the remaining points are not consistently different from the chosen model; the different, however, from the curve of production which the model predicts if there had been no p of high mixing rate—as shown by the dotted line. The dotted line can be checked against the valu the spring outburst in the years 1951-53 when there were no very high mixing rates; the range of values (Steele, 1956) is given by the bar in Fig. 9b.

In 1952 there was high mixing just after the spring outburst and this led to an increased su production in that year. This feature was fully discussed in the earlier paper (Steele, 1956) but for an period when high mixing rates occur—the autumn—the model provides insight which could not be at the time.

(1) 6 THE AUTUMN BREAKDOWN

There is a general assumption that an autumn outburst of production can be explained b breakdown of the thermocline bringing nutrients to the surface water. If the explanation were as s as this, then there would always be an autumn outburst. In fact, as the data from Fladen showed, is a great variability in the quantity of production during the autumn.

The breakdown of the thermocline is caused by two factors, cooling of the surface layer as the autumn resses and the effects of gales, particularly at the equinox. Because there are practically always high ds in October, cooling alone is never responsible for the breakdown; thus the important variable is timing of the gales. If they occur later in the season then, together with the cooling that has taken e, there will be a considerable mixing which will soon take the process to completion—that is, till column is homogeneous. This process can be imitated in the model by applying a high rate of mixing 10—to the steady state conditions typical of summer when the mixing rate was low—0·005. The lts of this are shown by the lower curve in Fig. 10; it can be seen that over 40 days there is only a t increase in the production rate and before such a time interval is completed, conditions would be ogeneous.

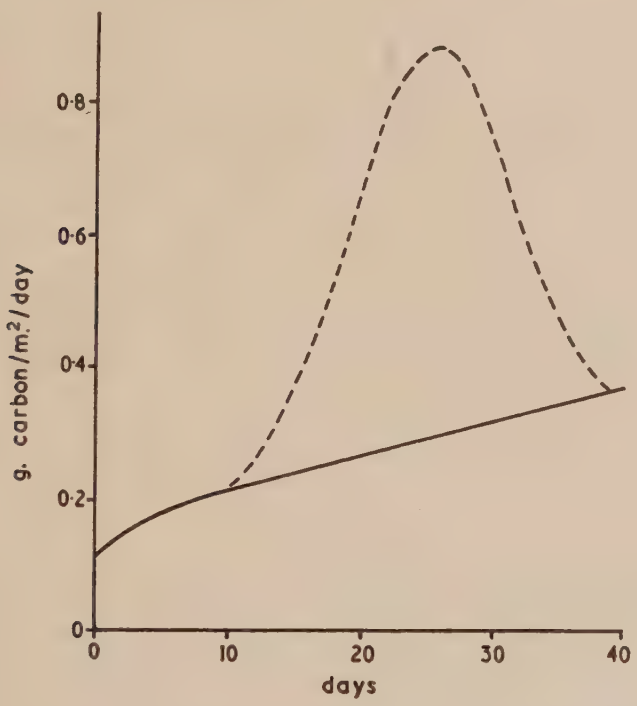

Fig. 10 The effects of a high mixing rate after low summer production.

nus a high rate of mixing in the autumn will not provide an outburst of plant growth. However, n a high rate is stopped after a short period, say ten days, and a low rate of mixing resumed, then is a sharp increase in the production rate as shown by the upper curve in Fig. 10, and this sequence provide an autumn outburst. In the mixing rates given in Table I there is such a sequence in and it was only for this year out of those considered that the phophate data showed a genuine rst in the autumn (Steele, 1956).

(1) 7 COMPARISON WITH OTHER DATA

The Inshore Stations

e Fladen data provide a check on the model for low rates of mixing. For a comparison of observed eoretical estimates of production when the mixing rate is high, the best data available are those he 'Inshore' group of stations sampled in 1953; in Table I the mean mixing rate is given. This not constant throughout the year but shows a minimum in summer. This feature is found quite

often at the more coastal stations and the increasing mixing rate in the autumn should correspon greater production. However, this increase is not necessarily an 'outburst' since it depends on the m rate being higher but not too high.

Fig. 11 shows the mean production histogram for the inshore stations. To save extra calculatio theoretical curve for $m = 0{\cdot}050$ is shown for the first 100 days together with a straight line to repr the summer condition when m is about 0·015.

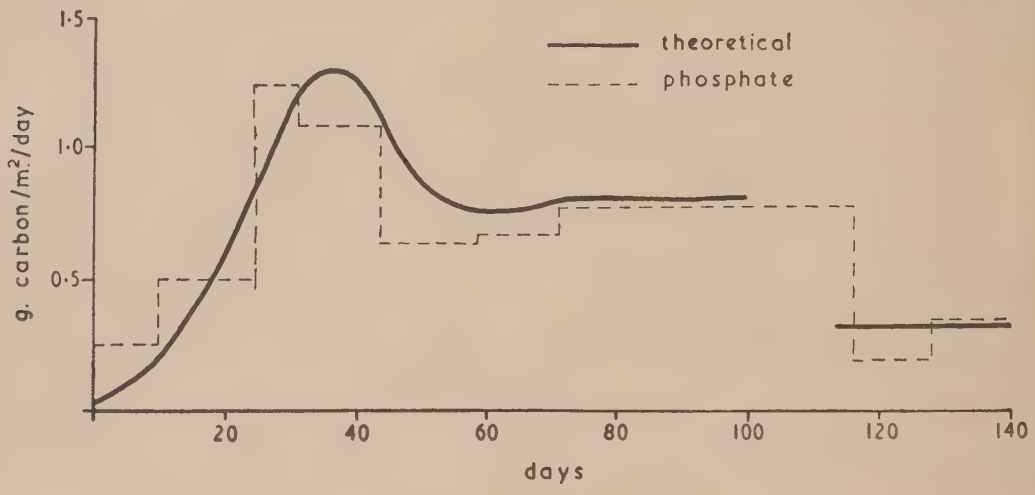

Fig. 11 The production cycle for the inshore stations in 1953.

At the Inshore group of stations, the thermocline lasts for just under six months and the four obs values for production in 1953 lay between 108 and 127 g/m² with a mean of 112 g/m². For mixing of 0·015 and 0·05, which is the range of the inshore stations, the theoretical values of production fo days are 72 g/m² and 140 g/m², and the inshore values are reasonably placed in this range. The f of 140 g/m² will represent the theoretical maximum yearly production to be expected in this area. unlikely, though, that this value will ever be achieved. Firstly because the mixing rate $m = 0{\cdot}05$ not be found continuously at any station and so the observed rates will be on either side of the ra maximum production. The second reason is that the model will start to break down in the shall waters with high mixing rates. The main feature of this breakdown will be that the concentrati phosphate in the lower water will be much less than that postulated, 0·70 μg.at./l. Thus mixing bring up less nutrient and the production will be less.

For these reasons, although no definite figures can be given, it seems likely that the regio maximum production will have conditions slightly more coastal than those shown by the inshore g and a yearly production of less than 140 g/m².

This suggestion does not take account of conditions close inshore where the depth is less than 5 In this region the water column will nearly always be homogeneous but, because of the shallow d production depends only on light and turbidity. Also, contact with the bottom and run off fro shore provide nutrients. Yet, except in particular cases such as river mouths, there seems no reas suppose that production will be very high.

(1) 7.2 Comparison of Other Variables

Fig. 12 shows the comparisons of observed and theoretical values of phosphate, plant carbo herbivore carbon for the two examples discussed in the previous sections. It can be seen that the phos data fit fairly well even for the more variable inshore stations. For the biological parameters, how

e is no real measure of agreement even when, with the group of inshore stations, the extremes of the iable range of values are taken into account; on the other hand there is no consistency in the rgence from the theoretical curves.

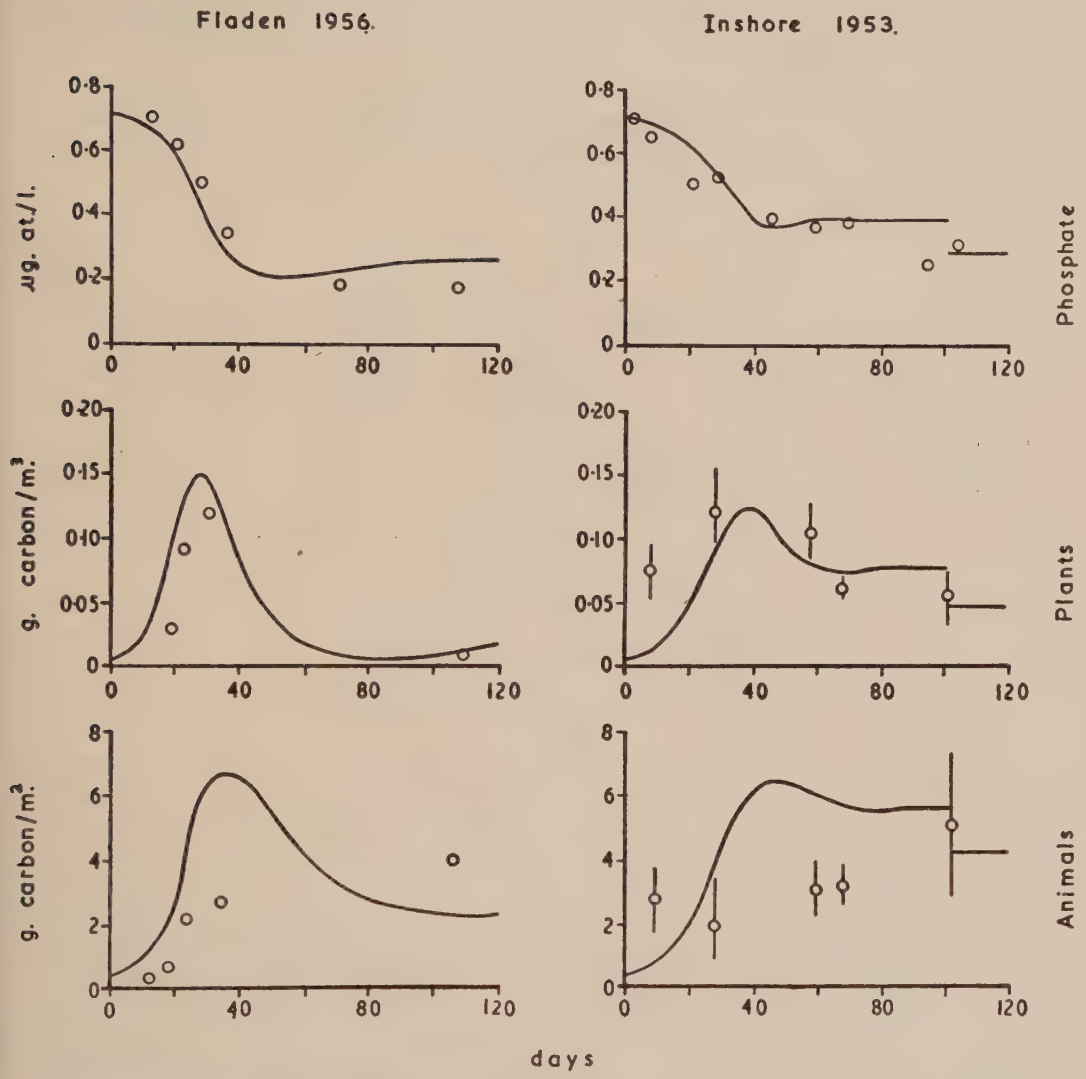

Fig. 12 A comparison of theoretical and observed values of (*a*) phosphate; (*b*) plants and (*c*) animals for Fladen 1956 and Inshore 1953.

n section (1) 4, it was shown that variations in photosynthetic rate have a much greater effect on ant population than on the production curves. This may be linked with the well-known "patchiness" rtoplankton to form a partial explanation of the lack of agreement between theoretical and observed s of the plant populations. Further, Cushing (1953) sets the confidence limits for *Calanus* in Hensen nuls at more than 30 to 300% which is an indication of the very approximate nature of zooplankton ing.

nere is also this difference between the chemical and biological samples; phosphate data represent dditive effects of changes over periods of time, whereas the biological data are "instantaneous" s. Perhaps these reasons will form some excuse for the almost random nature of the plant and animal vations.

(1) 8 CONDITIONS OVER THE NORWEGIAN DEEPS

The values of plant carbon just derived from the chlorophyll concentrations in two particular of the North Sea are not grossly inconsistent with the model. When a further area, the Norwegian D is considered, observed chlorophyll concentrations are very much higher than any predicted by model. This area is one where water of low salinity coming from the Baltic overlies more oceanic v and forms in early spring a stable layer which allows production to begin several weeks befor remainder of the northern North Sea. These high chlorophyll values are frequently found at the e March and the beginning of April and, as an example, the data at one of these stations is give Table II.

TABLE II

Data from 60°43′N 3°20′E on 30/3/55. Depth, 311 metres; time, 2100 hours; Zooplankton dry weight, 0·70 g/m²

Depth m	Temperature °C	Salinity ‰	Phosphate μg.at./l.	Plants g.carbon/m³
0	4·17	33·17	0·17	0·486
10	4·16	33·15	0·18	0·540
20	4·16	33·15		
30	4·18	33·14	0·19	0·594
40	4·19	33·14		
50	5·00	33·67	0·55	0·070
75	6·89	34·64		

The depth of the very stable layer was 40 m which is the value used in the model. The phosp concentration corresponded to that found in the model towards the end of the spring outburst. plant carbon concentration, on the other hand, had a mean of 0·54 g/m³, which must be compared a maximum in the model of less than 0·2 g/m³. Further, the carbon content of the zooplankton was low, 0·70 g/m² compared with an expected value of about 4·0 g/m²; such a low value is another fea common to these stations showing high chlorophylls.

It is obvious that these facts must be considered as a breakdown in the model as it has been use far. The problem is to what extent can the model be altered to predict these features and thus su an explanation of them?

It is unfortunate that the phosphate method of measuring production cannot be used in this (see section (2) 4) but there is no reason to believe that the productivity of these waters is very diff from the rest of the North Sea.

Given this, higher plant concentrations can be obtained in three ways: (*a*) higher photosynt rate; (*b*) lower sinking rate; (*c*) lower grazing rate.

(*a*) Since the production over the Norwegian Deeps occurs earlier than on Fladen, there wi less light and thus the photosynthetic rate should be less rather than greater.

(*b*) Due to the low salinity the density of the surface layer of water is less than on Fladen in the sp outburst, so in this layer the plants should sink as rapidly. It may be that the great change of de at the boundary of the two layers would slow down the sinking into the lower waters but, again, does not seem sufficient reason.

(*c*) The most obvious explanation, in view of the low zooplankton values, is that grazing is very m less than on Fladen.

o provide a further indication of the effect of grazing, and the lack of it, the curves in Fig. 13 have calculated. The lowest curve shows the normal conditions with low mixing. In the next curve ng is zero but the other factors are the same. In the highest curve both grazing and sinking are zero. Vhen there is no grazing in the upper layer the plant concentration is above the value of 0·20 g/m³ period of 22 days and thus within the range of the high values. On this basis a lack of grazing would ly explain the observations. When both grazing and sinking are zero the theoretical values obtained hen far too high.

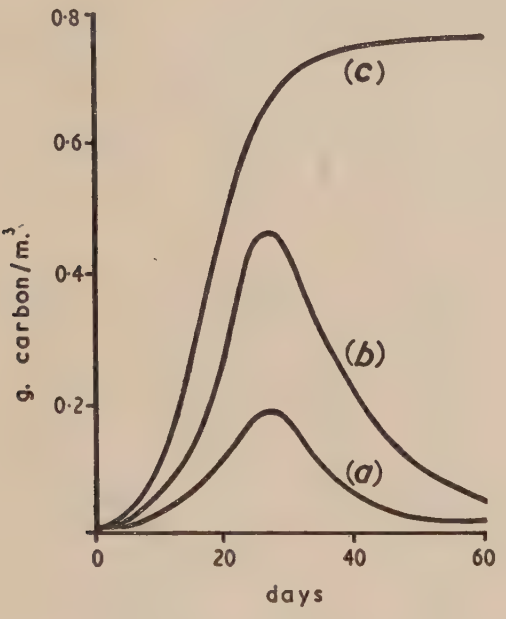

Fig. 13 The plant cycle with (*a*) normal conditions; (*b*) no grazing; (*c*) no grazing and no sinking.

Table II there is a further piece of evidence to be considered—the sudden drop in plant concen- n just below the upper mixed layer. Since the water from 50 to 75 m is fairly stable, this drop cannot ly explained by mixing. It might be due to a very slow sinking rate but it can also be explained ns of grazing if this grazing is limited to the water below the mixed layer.

ius the use of the model suggests two explanations: (*a*) low sinking rate; (*b*) almost no grazing in the mixed layer; of these the second seems the more probable. Further it should be possible to test hypotheses by (*a*) estimating production rate with C^{14}; (*b*) measuring the vertical distribution of oplankton.

s more difficult to give reasons for such behaviour of the zooplankton. That the copepods are present upper water is shown by Hardy Indicator hauls at 8 m depth (Glover, 1957) and they should also e to reproduce under these conditions as shown by experiments in Tromso Fjord (Marshall and 953). Such high chlorophyll concentrations, however, are not peculiar to the Norwegian Deeps. were also found (McIntyre and Steele, 1956) in the coastal waters off the west of Iceland and at the f the East Greenland current. In such regions, the production is due to stability caused by low r rather than high temperature. Thus it would seem that this feature is linked, by unknown means, particular set of hydrographic conditions.

s intended to make this problem the subject of future investigations.

(1) 9 THE EXPECTED PRODUCTION CYCLE IN THE NORTHERN NORTH SEA

The extent to which the model explains detailed events at two positions in the northern North has been described: for a third area—the Norwegian Deeps—an apparent breakdown occurs. Be this, however, there is the problem of providing a picture over a large area of the production cycle corresponding cycles of plants and animals.

The model has been so constructed that a knowledge of water movement and mixing throughou year should be sufficient to predict the cycle of production. For the northern North Sea, a simpl picture of the hydrography has been given (Steele, 1957a). Its main features are (*a*) during the p when there is a thermocline, which is the period when there is production, there is negligible horiz movement by the water below the thermocline; (*b*) during this same period there is a gradual westw spread of the less saline water which is caused by the turbulent lateral mixing of the current prod by the Baltic outflow with its axis off the Norwegian coast; (*c*) because of water mixed into this there is a slow drift of water down the western side of the area. These features of the surface move are shown in Fig. 14.

Fig. 14 A simplified picture of the main water movements in the northern North Sea.

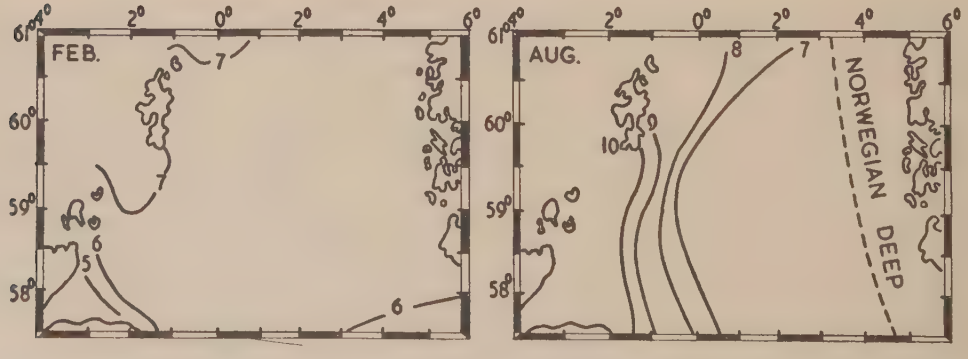

Fig. 15 Average bottom temperatures in the northern North Sea in winter (February) and summer (August).

For the bottom conditions, charts of mean temperature distributions will be used; these are in Fig. 15 (Deutsche Seewarte, 1927). Over the area considered, the winter (February) temper are fairly even and so the August values show the increase due to the downwards vertical mixing of w water. Thus the August contours may be used as an index of vertical mixing in the area.

his brief outline will be used to discuss the expected effects of water mixing and movement on uction.

irstly the westwards surface mixing from the Norwegian Deeps will carry water in which the nutrients ow, since production in this area has been going on for about a month before the movement starts. change begins when the water to the west becomes stabilised, in other words at the beginning of roduction cycle in this more westerly area. Thus at its start water of low and high phosphate content e mixing together. Yet, since the general rate of westerly movement is not great, there will not been much mixing before the westerly water has also passed through its spring outburst and reached itions similar to those at its eastern edge, so that the effects of mixing will be noticeable only in a strip on the edge of the Norwegian Deeps. But elsewhere the waters which are mixing, although of ent salinities, will be in a similar state so far as the production cycle is concerned.

he southerly flow down the western side of the area will bring in water from the north of Shetland, ı has been subject to oceanic conditions and so anomalies can be expected to the east of Shetland. ıd this area, the general direction of flow (Fig. 14) corresponds to the bottom temperature contours 15) and so the movement is along lines subject to the same conditions of vertical mixing.

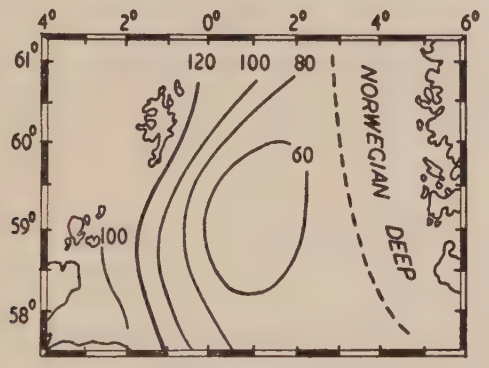

Fig. 16 Expected yearly production of organic carbon (g/m²).

ı this basis it would appear that the effect of the lateral movements is to produce small areas which oset the model based on purely vertical mixing, but that in general it should not affect this model sly. Using the theoretical model it is then possible to produce a chart showing approximately the ed yearly production of organic carbon (Fig. 16).

e region to the east of the dotted line corresponds to the area of the Norwegian Deeps in which ain feature is the very early spring production. For the remaining area, the principal points are the spring there will be no great difference in production, but the offshore production should have ıer but narrower peak; (*b*) it is the summer production rates which are mainly responsible for riations in the yearly totals; (*c*) in the autumn, the production cycle ends earlier inshore but there e quite large production later in the offshore waters.

general, the inshore waters where mixing is dominated by tide have a high total production more evenly, but finishing fairly early; the offshore waters have a lower production with greater al variation and, since mixing is mainly controlled by the occurrence of gales, the year to year ction is much more variable.

is from the point of view of this broad outline based on theoretical considerations that a detailed gation will be made of data collected on surveys carried out during 1954-56.

Part Two

OBSERVATIONS IN THE NORTHERN NORTH SEA

For the three years 1954-1956 surveys of the northern North Sea were carried out several time year. They were fitted in with other work in the laboratory and so the dates of the cruises are not same from year to year; further, due to the usual difficulties such as weather, many of the cruises w not completed.

For these reasons it is not possible to make a complete and strict comparison among the three ye The data have to be handled in a piecemeal manner; for some aspects a comparison is possible, but others it is necessary to take the three years together to obtain a rough average. The difficulties are m awkward in the actual estimates of production from the phosphate data. The estimate is obtained calculating the water-mixing between two dates and using this to remove the effects of mixing from observed phosphate changes. Thus the value for the "biological change" in phosphate depends observations made both at the beginning and the end of the interval and the method is most success when the time interval between sampling is not too great.

The cruises were arranged to take place about (i) March-April; (ii) May-June; (iii) July-Augu (iv) September-October. The three intervals of two months between each pair of cruises should giv value for spring, summer and autumn production.

(2) 1 TEMPERATURE AND SALINITY DATA

The hypothesis that, from April to September, the lateral water movement below the thermocl is negligible has an obvious bearing on the phosphate estimates of production, so a detailed study wil made of the charts of near-bottom temperature and salinity (Figs. 17, 18 and 19) for the three y 1954-56 to see how far this hypothesis is verified.

From March to April 1954 there is a southward movement of the 35·30‰ isohaline which probably indic the last stages of the winter inflow; but from April to June there would appear to be very little change in salinities. The regression of the 35·30 isohaline between June and August may be due to the mixing downwa of the less saline surface waters, or to lateral mixing of the lower waters.

In both 1955 and 1956 there are southerly water movements shown by the changes in the 35·20 isohali From May to June the problem raised by these changes is not to explain where the water comes from but wh the displaced water goes. Thus from May to June 1955 both temperature and salinity suggest that the displa water formed a tongue extending north-eastwards along 1°E. The separation in June and July of the south patch of water with salinity greater than 35·20 may again be explained by lateral mixing.

A similar explanation seems needed for the patch of higher salinity water in the north-east in May 1 which is all that remains of this tongue found in April.

Perhaps the feature which is most difficult to explain is that of 35·30 isohaline in October 1956. There i very large change in the position of this contour from July-August, yet it is difficult to accept a general incurs of water from the north-east since its temperature in August was over 9°C whereas in October much of the a where the salinity is greater than 35·30 still has a temperature lower than 8°C. However, the change in sali is comparatively slight over much of the area; this is due to the fact that whereas the salinity in August just below 35·30, in October it was just above it in an area shown by the dotted line. This increase of sali by about 0·03-0·04 corresponds to a temperature rise of about 1°C and once more it is easiest to think of lat mixing as the explanation.

In all these years the temperatures show that the whole central mass remains almost unchanged a it is this relatively heavy water which acts as a barrier and prevents these intrusions from being o large scale, though there are small movements of bottom water along the line shown in Fig. 14 wh correspond to the surface movements mentioned in the previous section. These movements occur abo May-June and result in slight northward displacements of the water to the east of the line. The importa

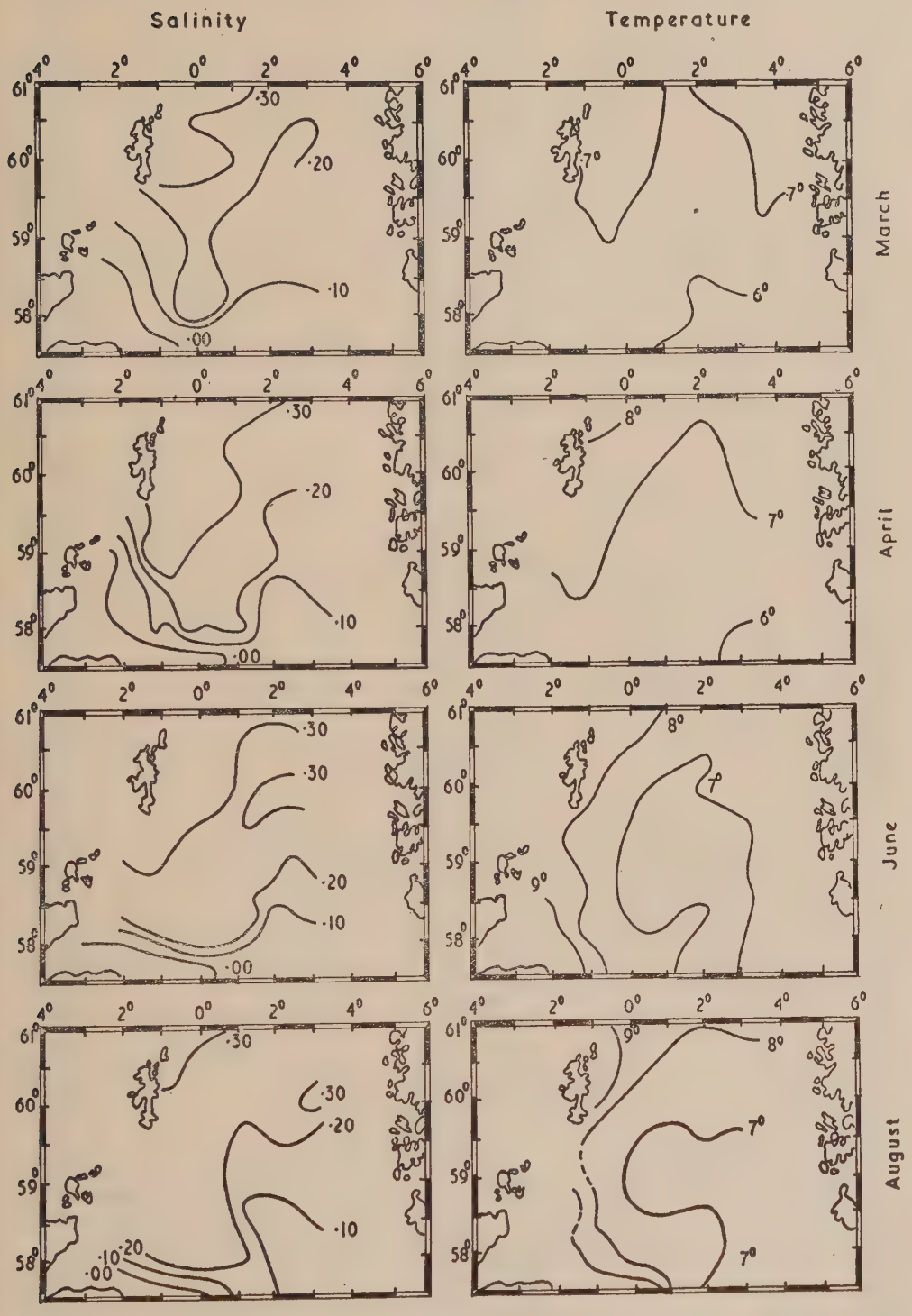

Fig. 17 Salinity and temperature near the bottom of the northern North Sea in 1954. (In this and the next two figures, conditions in the deep waters near Norway are omitted; any other areas omitted are shown by a dashed boundary. The salinity values are 35‰+).

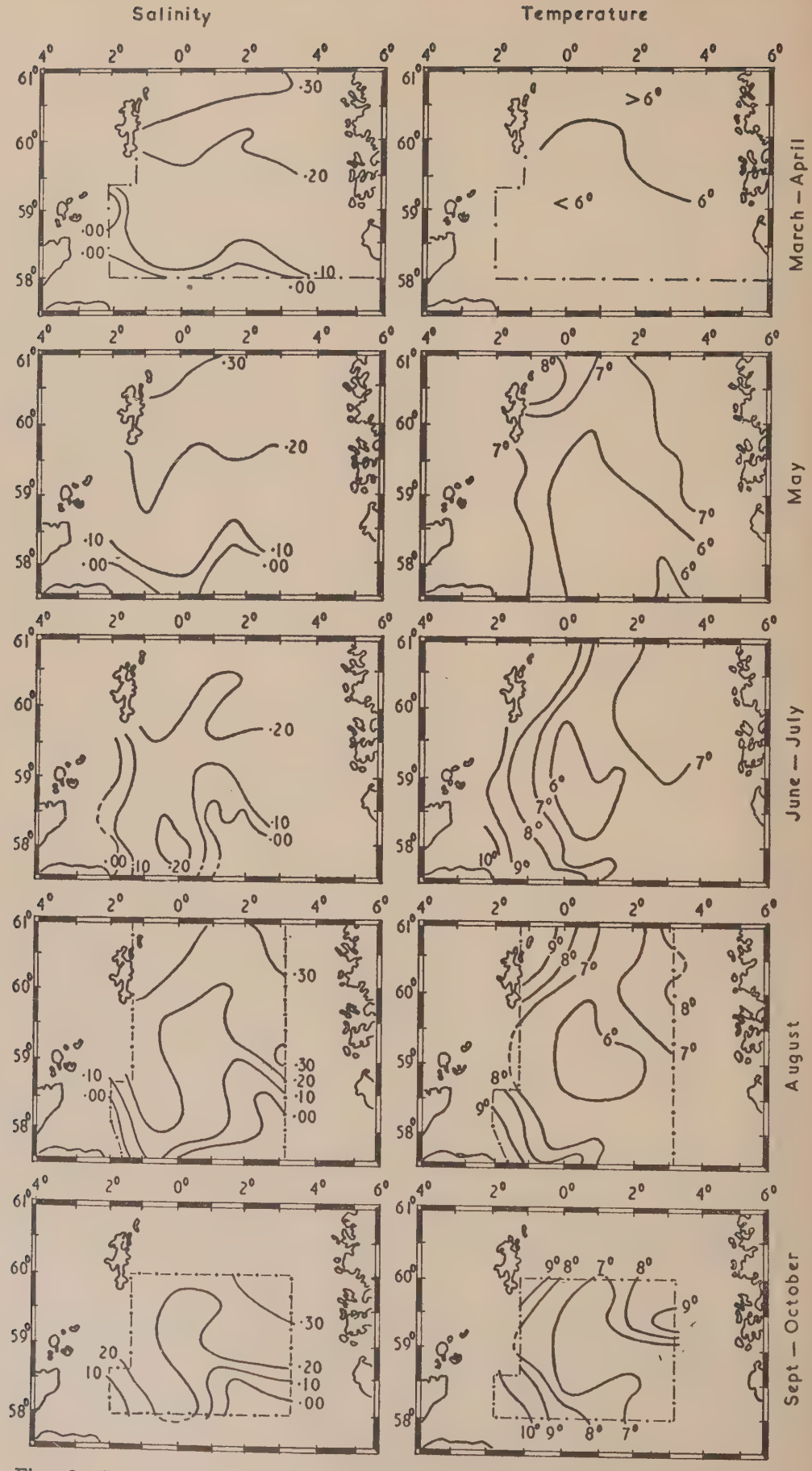

Fig. 18 Salinity and temperature near the bottom of the northern North Sea in 1955.

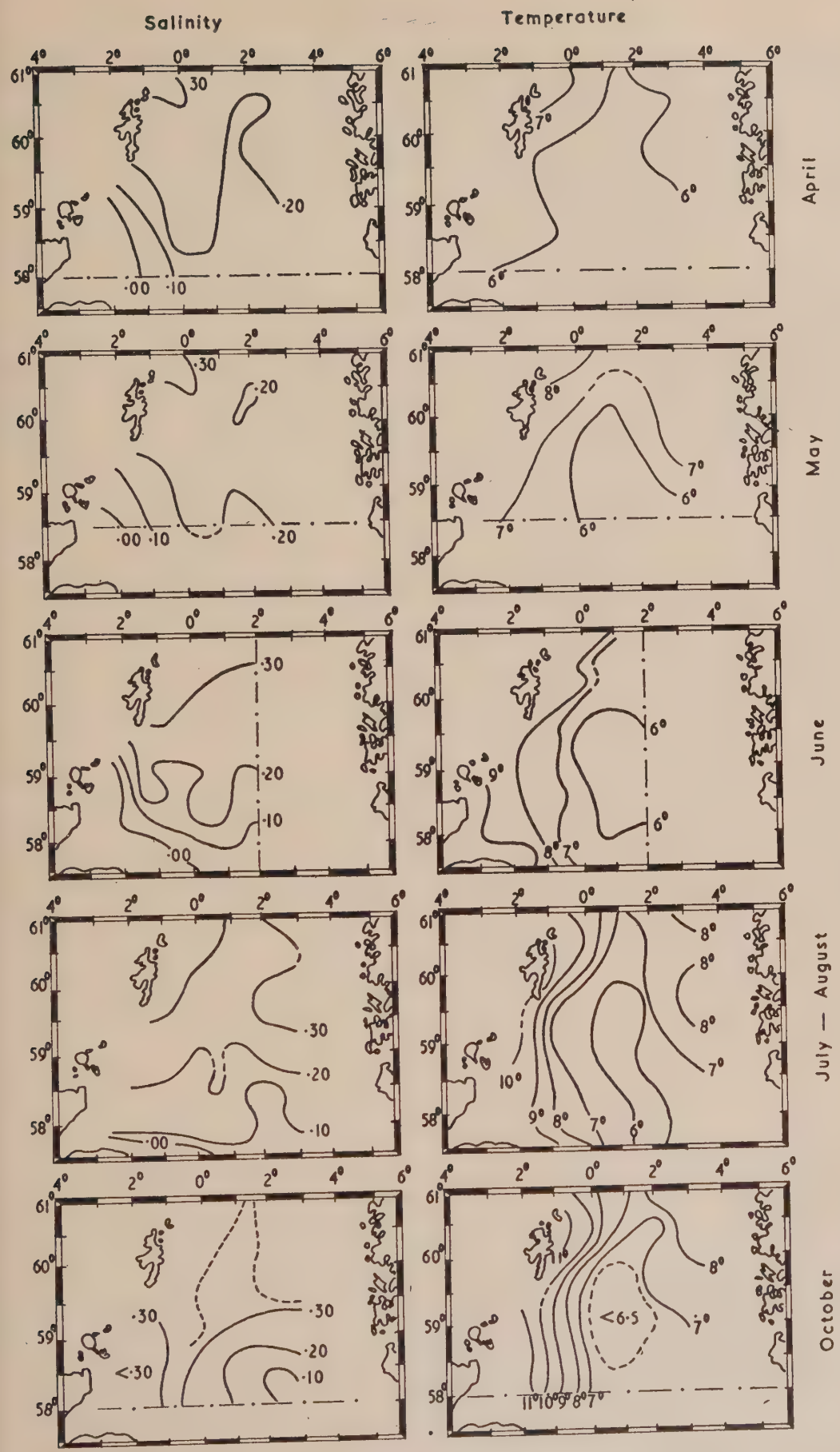

Fig. 19 Salinity and temperature near the bottom of the northern North Sea in 1956.

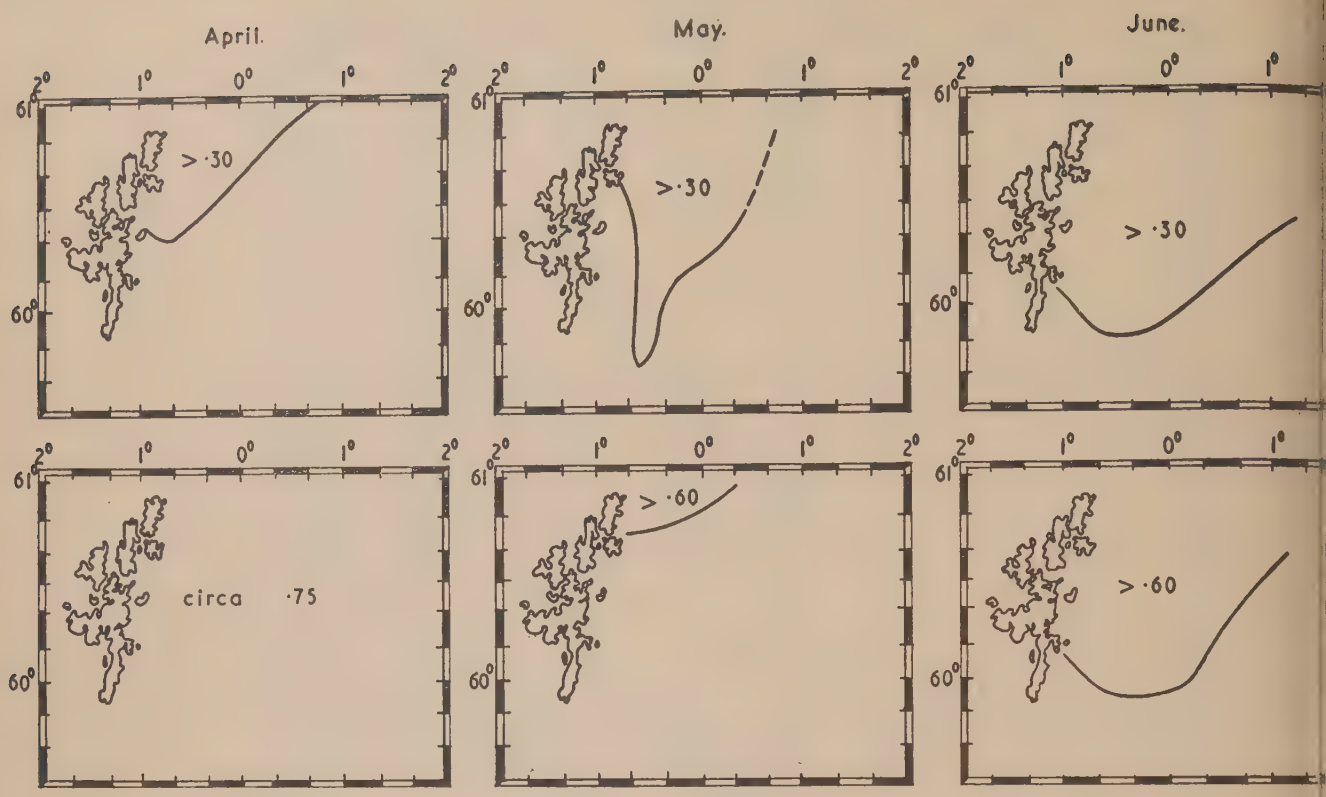

Fig. 20 Regions of high salinity and phosphate to the east of Shetland in 1956.

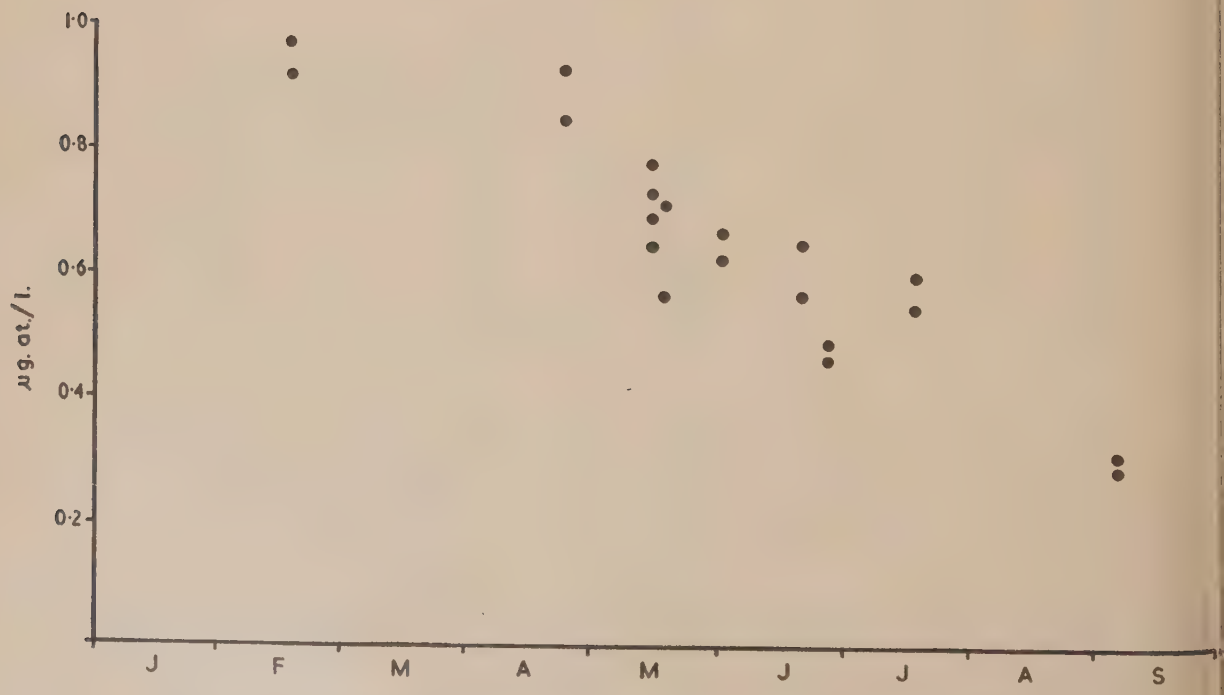

Fig. 21 Values of surface phosphate in the Faroe-Shetland Channel to the north-west of Shetland for the years 1951-55.

f these changes is that they occur along temperature contours. This is to be expected since with l salinity changes involved temperature contours will correspond roughly with density contours. her result of the variations in salinity and vertical mixing is that, whereas in the early spring es of salinity correspond to differences of temperature, by the summer the contours are often angles to each other; thus the movement of water along lines of constant temperature will produce in salinity at any position. It is for the reasons given that these changes in salinity are not ed important in relation to the assessment of production at any particular station.

concept of similar mixing breaks down in the north-west corner where the mixing water has ie over the continental shelf and so has an 'oceanic' past. In 1956 this can be seen by the n of the area of water with salinity higher than 35·30 and its effects are shown by the surface in phosphate (Fig. 20). The area in June with phosphate concentration higher than 0·60 μg.at./l me as the high salinity region and the explanation of an increase in phosphate concentration is a study of conditions to the north-west of Shetland in the deep waters of the Faroe-Shetland where concentrations of 0·60 are normal for June (Fig. 21).

e is one further hydrographic feature to be pointed out. In June 1954, August 1955, September- 1955 and July-August 1956 patches of water with high salinity and high temperature occur on ern edge of the area surveyed. This water, which is of Atlantic type, comes from the Norwegian here there is a slow mid-water inflow from the Norwegian Sea, probably as a replacement for ixed upwards into the Baltic outflow. Again this must be expected to upset the production s and this will be discussed when these estimates are given.

neral conclusion of this study is that it appears to be necessary to postulate lateral mixing as a nt feature of the changes in the lower water.

(2) 2 CHEMICAL DATA

as shown earlier by the model, surface phosphate concentration is not a generally good index ction. It can show, by the low values found, that production starts earlier over the Norwegian an elsewhere. But this feature can be deduced from the hydrographic data which show that ace layers are stable and it is even more obvious from the high chlorophyll concentrations.

larly, surface oxygen concentrations are not very helpful in estimating production. The fact y may be above the equilibrium concentrations can indicate either production or a recent in surface temperature.

ts of these quantities are most useful in the discovery of anomalous features such as that d in the previous section. For the years studied here, the charts and a general description are Johnston (1956) and Burns (1957, 1958).

(2) 3 CHLOROPHYLL AND DRY WEIGHT DATA

variability of plankton samples has been shown already in section (1) 7.2. Thus the study of the istribution of plants and animals is concerned with the general pictures provided by the sampling. chlorophyll, estimates of the mean values in the euphotic zone were obtained by averaging the ations at 10 and 30 m and these values were then converted to carbon using the conversion ven in section (1) 1.2. In Fig. 22 the March and April-May charts show the general levels of ation found in the three years but for the other two charts the actual contours for the compara- mplete surveys made in 1956 are used.

first two charts show the general features discussed in previous sections; the range, 150-250 n April-May, corresponds to the normal peak of the spring outburst whereas in the earlier chart mg/m^3 contour indicates the general area where the exceptionally high values are usually found.

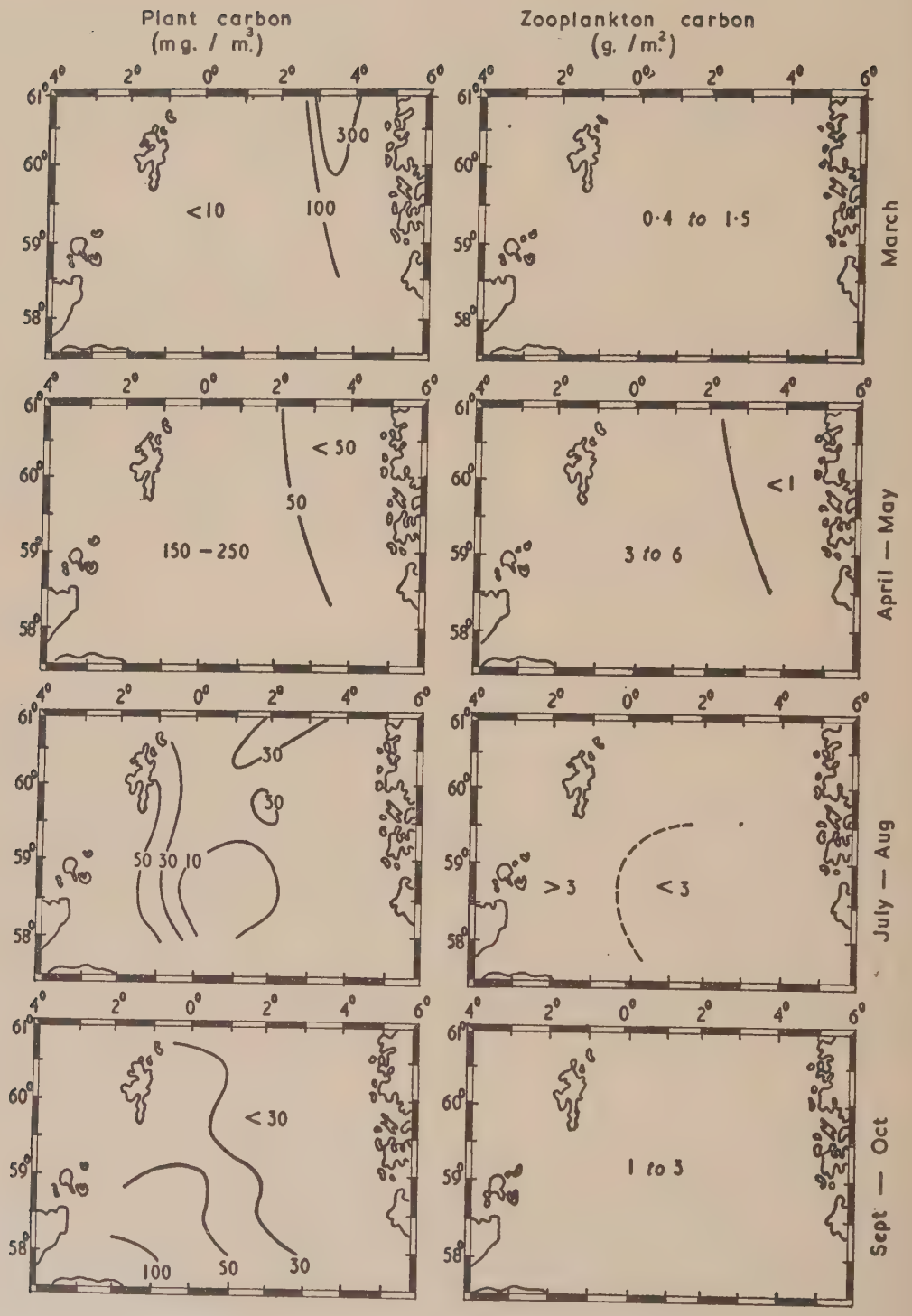

Fig. 22 The distributions of plants and animals.

he summer contours agree fairly well with the distribution expected from the theoretical study of uction and the range of values from 10 to over 50 mg/m³ is close to the range of values in Fig. 5.
he autumn conditions show a general but not dramatic increase in population. The distribution, ver, is irregular and dependent on the stage which the autumn breakdown has reached; thus ugh the population has doubled at 58°N 2°W, at 59°N 2°W it is quite small compared with summer, o the complete breakdown of the thermocline at that position.
n this way, both in distribution and in range of values, the chlorophyll data provide reasonable rns which agree with the model quite closely. For the carbon content of zooplankton, there are ly any patterns and the most that may be said is that the range of values, although rather low, is e same order as that predicted by the model. However the quantitative distributions of Calanus, as n by the Hardy Indicator hauls taken at 8 m (Glover, 1957), agree roughly with the expected butions. In the summer they show maximum populations in a north-south strip on the western side e area; the axis of this strip is rather more off-shore than the contour of expected maximum uction and this would follow from the usual view that the populations are also determined by the of 'Atlantic' water.

(2) 4 ESTIMATES OF PRODUCTION

he calculations for production from the phosphate data were made in the way described in the r paper (Steele, 1956). In Fig. 23 the results of these calculations are given for the three years ·56. The seasons were chosen to begin and end at the following dates: spring—until 30th May; ner—1st June to 10th August; autumn—11th August onwards. In this way results from the different could be compared and so the individual values were adjusted accordingly; for example, when a g' value was for the period until 10th June then a figure was subtracted corresponding to ten the daily summer rate for that station. Certain of the results have been omitted and others appear alous; these will be discussed first.
or spring 1956, the calculations are obviously meaningless in the northerly area where there was arge increase in surface phosphate concentration shown by values higher than 0·6 μg.at./l. This re was discussed earlier, section (2) 1, and explained by the intrusion of oceanic water in June.
n spring 1955 two very high values are found—indicated by the 'boxed' figures. Technically, these ue to an apparently high rate of mixing shown by large increases in the bottom temperature in May 19). But from the model we know that great mixing does not provide greatly increased production alues for the spring in the region of 70-80 g/m² are impossible. Thus these values must be explained similar influx of warm oceanic water occurring before May and so before the phosphate values reduced.
hese two anomalies cast doubt on other values from this area. The comparatively high summer uction, especially the partly 'boxed' value, may be due also to a warming of the lower waters caused teral movement rather than by vertical mixing. It is important, however, to recognise that this could be expected on the basis of the hydrographic data.
imilarly a study of the hydrography indicates an explanation for the other main region where alies are found—the values occurring along the edge of the Norwegian Deeps. These occur mainly 55 when the summer and autumn sampling in this area was most extensive. The 'boxed' value of g/m² in summer 1955, can be checked against the model; the observed figure gives a daily mean of 1·8 g/m²/ day which is more than twice the optimum rate predicted by the model. Then again, alue of 61 g/m² in the same season, although a possible value, is also in an area of intrusion of warm water from the Norwegian Deeps (Fig. 18). This intrusion had increased by October and so the d' values for the autumn are also dubious.
he opposite effect of this intrusion is shown by the decrease from June to August 1954 in the size of atch of water with salinity greater than 35·30‰. The associated drop in temperature meant that lations were impossible at the station marked by a cross (Fig. 23) in summer 1954. A similar naly occurred at the station marked by a cross in the autumn 1955. It is difficult to say whether this actually 'disappears' or is merely shifted, perhaps by the movements discussed earlier, section (2) 1.

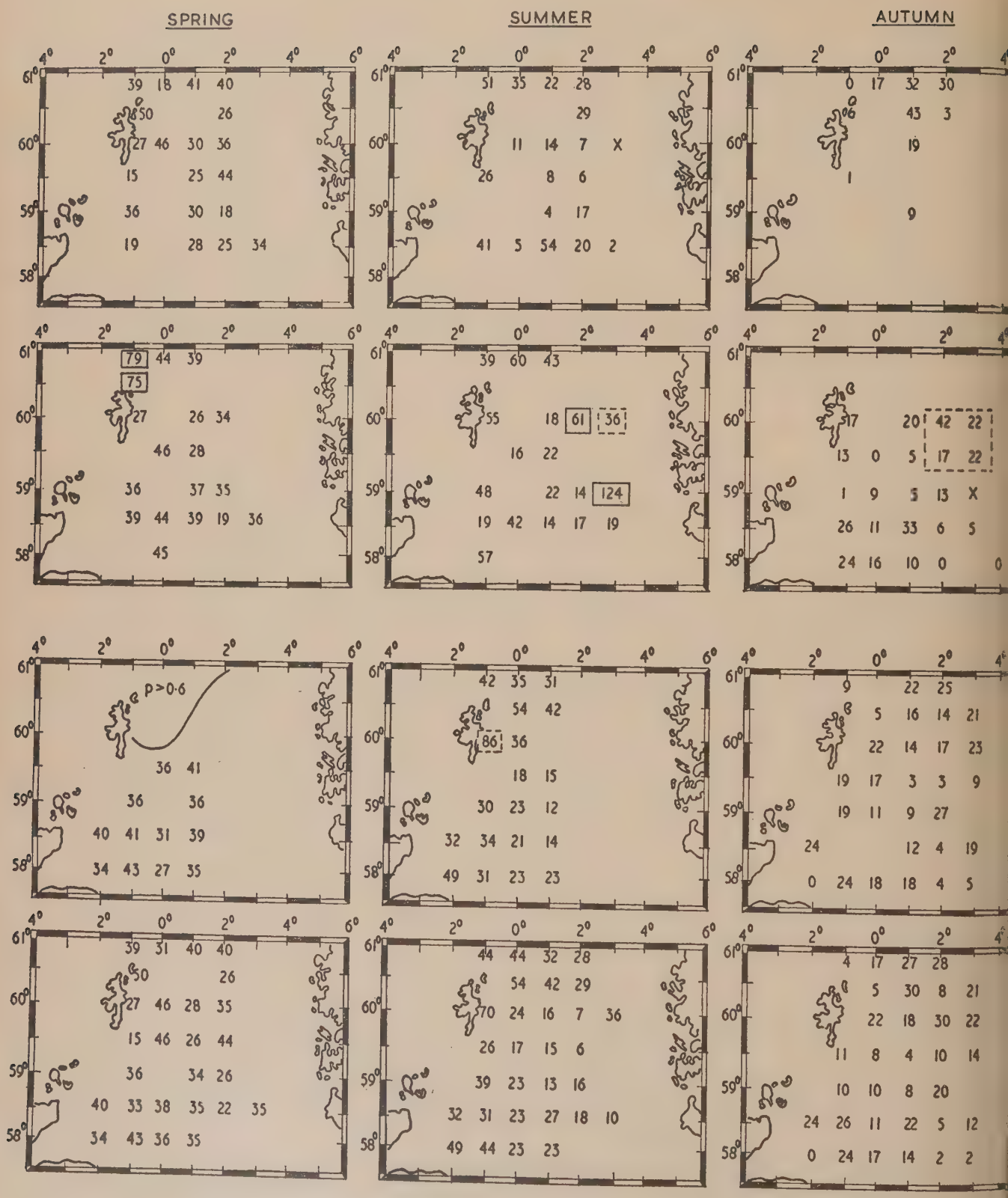

Fig. 23 The seasonal production of organic carbon (g/m²) estimated from phosphate for the years 1954-56, together with the mean seasonal values.

er, these complementary effects of sudden increases and decreases in temperature and salinity ate the estimates of production in this region.

producing the mean values of production for each season (Fig. 23) the completely 'boxed' values en omitted but the partly 'boxed' ones retained. It is obvious that these means are not particularly ant since there is often a wide range of values for any particular station, but it is only in this way e partial results for each year and season can be drawn together to give an adequate series of s for the whole area.

(2) 5 COMPARISON WITH THEORY

mparison of the theoretical model with the phosphate estimates is not completely straightforward e two methods have some common features. The phosphate estimate is essentially a calculation hosphate used in the euphotic zone and is based partly on observed values for vertical mixing ater. This same upwards mixing of phosphate is one of the relevant factors for the model and for ethods it is necessary that the effects of lateral movements should be negligible.

difference in the methods is that the phosphate estimates are a direct relation of carbon and orus based on the comparatively complex distributions of phosphate and temperature; whereas model the hydrographic conditions are very much simplified and the phosphorus affects the e of production indirectly through its control of photosynthetic rate.

these reasons, it is not possible to have a direct check on the values for production alone; what ded is a more complicated comparison of the observed salinity, temperature and phosphate and the production rates derived from them, with the simplified outline of the hydrography model based on this outline.

is supposed that the spring outburst starts near the middle of April then the time allowed here 'spring'—46 days approximately—is close to the period of 44 days by which time the high and ing rates had given equal totals of production (Fig. 7). On this basis the expected values for the eriod should be nearly all the same. Fig. 23 shows that although there is variability, there is no in these variations. The mean value of all the spring estimates is 35 g/m² which is near the expected see Fig. 7 and Fig. 9. (It should be remembered that certain very high values have been omitted).

the summer, the mean values are an adequate description of the general trend of values found year and they stress the feature suggested by the model; that at this time major variations in ion will occur and these variations should correspond to the contours of bottom temperature or August in Figs. 17-19.

the autumn, the values are extremely haphazard. The dates of sampling were usually in the last September and the first two of October, so that the data may have been collected before, during the autumn breakdown. The study of the mechanism of this breakdown suggested that, for ion at this period, week to week changes in mixing were important. Thus, to detect the effects luction, fairly detailed sampling is necessary, for once the water column becomes homogeneous, nges have been so great that the method of estimating mixing breaks down. For this reason it is y to rely on the model for guidance as to the autumn production. It implies that there is no autumn outburst inshore, but the high rate of production continues till the breakdown which efore the end of September. In the more offshore waters, with less but still significant tidal effect, an increased rate of mixing which increases production and ends about mid-October. For the area, autumn production depends on gales and here, in suitable circumstances, there can be a autumn outburst at the end of September and beginning of October.

he south east of the area surveyed, due to a combination of small tidal effect and great stability per water of low salinity, there is negligible mixing even at the beginning of November and so a may nearly always have a low autumn production. These conditions may apply to parts of the tral North Sea.

lly, given these various deficiencies, the values for the three seasons may be added together to hart of the mean yearly production (Fig. 24), and this may be compared with the distribution

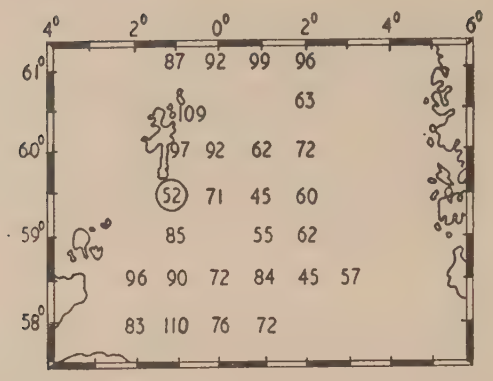

Fig. 24 The estimated mean yearly production of organic carbon (g/m^2) for the years 1954-56.

given by the model, Fig. 16. With the exception of the 'circled' value, the two are in rough g agreement. Particularly, the observed range of values, 45 to 110 g/m^2, lies within the range predic the model.

DISCUSSION

During the three years 1954-56, a very large mass of data was collected concerning the hydrog chemistry and plankton of the northern North Sea. Any small part of that mass contains unexp anomalies: a single unexpectedly high chlorophyll concentration, a dubious temperature. It obviously be impossible to discuss each of these values and, although some are mentioned, any a such as has been given here, must contain a large number of concealed decisions concerning the v of particular samples.

Similarly, in the mass of experimental evidence concerning plant and animal behaviour the numerous anomalies. When hypotheses are chosen, they depend on a choice from among these con tions. Even here it is impossible, in a reasonable space, to state all the evidence, so that these de also are partly concealed.

There is, then, a basic choice about what is important and unimportant. In this paper, the towards a very simple set of postulates which can be fitted into a mathematical scheme and u explain events in a chosen area; the background of this choice has been discussed in another (Steele, 1959). It is certain that the simplicity described by the postulates will not in fact be realise use of this approach is to discuss merely the extent to which it holds. It can point to the conditions it breaks down and suggest the methods and alternative hypotheses for further investigation.

The model is based largely on data collected in one area, the Fladen Ground in the centre northern North Sea. It is thus mainly applicable when vertical mixing is not too great and so it expected to break down in coastal waters. From evidence of events to the north-east of the Sh Islands the model cannot be applied in this area since some of the water is of 'oceanic' origi implication is that the model does not apply to oceanic conditions. This also is to be expected sin depth of the thermocline in these waters is very different from that on the Continental Shelf and of the main factors controlling production (Sverdrup, 1953).

Finally, the model appears to break down over the Norwegian Deeps and this is not expecte the model can be used to suggest new postulates that can be tested in this area.

These features illustrate the limitations of the model but the general agreement between exp and calculated yearly production suggests that the model is a reasonably acceptable representati conditions over the greater part of the area.

Beyond this, the abstract nature of the units used in these production studies makes it diffic imagine the detailed steps to the higher trophic levels where the study of the species involved c

be neglected. This difficulty is particularly serious when the attempt is made to relate the study uction to the problems of the fisheries; it is often possible to find apparent correlations but such isons are of very dubious value. For example, during the year in the northern North Sea the of maximum production are successively:

(1) the Norwegian Deeps in March-April;
(2) the remaining area during the spring outburst in May;
(3) the western coastal waters during the summer;
(4) the deeper offshore waters in late autumn.

s cycle corresponds to the generally accepted migrations of autumn spawned herring in the Banks' stock) but this movement can also be related to the current system and probably to a host factors.

ain, the chart of yearly production shows fair agreement with the variations in growth rates of k (provided by my colleague R. Jones), the smallest rates corresponding to areas of lowest produc- ut this pattern is also found in the bottom temperatures, and so the growth rates may be linked with feeding or with metabolic processes—or, once more, with some other unknown factor.

h patterns are a useful source of ideas in the search for the underlying casual relations between n and fish. There is, however, no simple quantitative comparison between basic production and nmercial fisheries since the phytoplankton produced can go to support humanly useless forms of iley, 1955). On this basis high production is a necessary but not a sufficient condition for nically useful supplies of fish, and the investigation of the complex pathways between the environ- nd the fisheries cannot be avoided. This study of primary production is a first step towards putting nplex on a quantitative basis for the northern North Sea.

SUMMARY

athematical model of the plant production cycle is set up and is used to study the effects of varying ters, principally vertical mixing.

theoretical estimates of production are in good agreement with detailed observations in two ut do not explain data from the Norwegian Deeps.

this basis a chart of expected values of production from the northern North Sea is constructed.

ee years of observation in this area are described and the production estimated from phosphate he range of values and the general distribution agree with the model.

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